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1973–1974

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CONTENTS OF VOLUME 18

Number		Page
1–2.	THE TABANIDAE (DIPTERA) OF LOUISIANA Mac A. Tidwell	1
3.	THE SYSTEMATICS AND EVOLUTION OF THE GENUS *CHIROSTOMA* SWAINSON (PISCES, ATHERINIDAE) Clyde D. Barbour	97
4.	A NEW SPECIES OF MAP TURTLE (GENUS *GRAPTEMYS*) FROM THE GUADALUPE RIVER SYSTEM IN TEXAS David Haynes and Ronald R. McKown	143
	AN ECOLOGICAL STUDY OF THE QUEEN SNAKE, *REGINA SEPTEMVITTATA* (SAY) IN KENTUCKY Branley A. Branson and Edd C. Baker	153
	ETHEOSTOMA BOSCHUNGI, A NEW PERCID FISH FROM THE TENNESSEE RIVER DRAINAGE IN NORTHERN ALABAMA AND WESTERN TENNESSEE Benjamin R. Wall, Jr. and James D. Williams	172

TULANE STUDIES IN ZOOLOGY AND BOTANY

VOLUME 18

INDEX TO AUTHORS AND TAXA

Note: The Tabanidae of Louisiana are indexed on page 94. The genus *Chirostoma* is indexed on page 97. These indexes are not included here. New taxa are in boldface.

Baker, Edd C., article, 153
Barbour, Clyde D., article, 97
Branson, Branley A., article, 153

Cambarus sp., 157, 158
Campostoma anomalum, 181
Catostomus commersonii, 181
Chrosomus erythrogaster, 181
Clinostomus funduloides, 181
Cottus carolinae, 181
Crotalus atrox, 160
Cryptobranchus alleganiensis, 168, 170

Erimyzon oblongus, 181
Esox americanus, 181
Etheostoma **boschungi**, 172 ff.
Etheostoma caeruleum, 181
Etheostoma cragini, 172, 173, 180, 181
Etheostoma duryi, 181
Etheostoma flabellare, 158, 181
Etheostoma pallididorsum, 172, 175, 180, 181, 182
Etheostoma punctulatum, 172, 181
Etheostoma simoterum, 181
Etheostoma squamiceps, 181

Fundulus catenatus, 181
Fundulus olivaceous, 181

Gambusia affinis, 181
Graptemys barbouri, 150
Graptemys **caglei**, 143 ff.
Graptemys kohni, 150, 151
Graptemys pseudogeographica, 151
Graptemys pulchra, 150
Graptemys versa, 150, 151

Haynes, David, article, 143
Hemitremia flammea, 181
Hypentelium nigricans, 181

Lampetra aepyptra, 181
Lepomis cyanellus, 181
Lepomis macrochirus, 181
Lepomis megalotis, 181

McKown, Ronald R., article, 143
Micropterus punctulatus, 181

Natrix sipedon, 154, 157, 164, 165, 167
Notropis ardens, 181
Notropis chrysocephalus, 181

Orconectes juvenilis, 157, 158, 159, 169
Orconectes obscurus, 159

Pimephales notatus, 181
Placobdella rugosa, 169, 170

Rana sp., 157
Regina grahami, 154, 161
Regina septemvittata, 153 ff.

Semotilus atromaculatus, 181

Tenebrio sp., 157
Thamnophis sirtalis, 161, 165
Tidwell, Mac A., article, 1

Verticellium, 169, 170

Wall, Benjamin R., Jr., article, 172
Williams, James D., article, 172

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THE TABANIDAE (DIPTERA) OF LOUISIANA

MAC A. TIDWELL

Department of Zoology and Physiology, Louisiana State University, Baton Rouge, Louisiana 70803

p. 1

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CONTENTS

ABSTRACT 2
INTRODUCTION 2
ECONOMIC ASPECTS 2
LIFE HISTORY 3
ECOLOGICAL ASPECTS 3
COLLECTING METHODS 8
REARING AND PRESERVATION OF IMMATURES 8
LARVAL MORPHOLOGY 9
ADULT MORPHOLOGY 11
KEYS TO THE TABANIDAE 12
KEY TO GENERA OF THE LARVAE OF TABANIDAE 12
KEY TO FULL-GROWN LARVAE OF *Chrysops* 13
KEY TO FULL-GROWN LARVAE OF *Tabanus* 15
KEY TO GENERA OF ADULT TABANIDAE 17
KEY TO FEMALES OF *Chrysops* 19
KEY TO MALES OF *Chrysops* 25
KEY TO FEMALES OF *Tabanus* 28
KEY TO MALES OF *Tabanus* 33
KEY TO SPECIES OF *Hybomitra* 37
KEY TO SPECIES OF *Agkistrocerus* 37
KEY TO SPECIES OF *Hamatabanus* 38
SPECIES ACCOUNTS 38
GENUS *Merycomyia* HINE 38
GENUS *Silvius* MEIGEN 39
GENUS *Chrysops* MEIGEN 39
GENUS *Diachlorus* OSTEN SACKEN 64
GENUS *Stenotabanus* LUTZ 64
GENUS *Chlorotabanus* LUTZ 64
GENUS *Whitneyomyia* BEQUAERT 65
GENUS *Leucotabanus* LUTZ 64
GENUS *Tabanus* LINNAEUS 66
GENUS *Hybomitra* ENDERLEIN 89
GENUS *Agkistrocerus* PHILIP 90
GENUS *Hamatabanus* PHILIP 90
ACKNOWLEDGMENTS 91
REFERENCES CITED 91
ADDENDUM 93
INDEX TO SPECIES ACCOUNTS 94

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Abstract

A study to elucidate some aspects associated with tabanid populations was conducted with an emphasis on systematic relationships. Distribution of the Louisiana Tabanidae was correlated with six major ecological regions which were defined primarily by the characteristic vegetational forms.

Approximately 18,000 adults and 1000 larvae were collected from Louisiana and neighboring states. Twelve genera and 100 species and subspecies are recorded for Louisiana. Taxonomic keys, distributional data, and ecological information are given for the species. Emphasis is placed on phenotypic variation in local populations and intergradation in certain species complexes. Changes in the taxonomic status are included for four species and a new species is described.

Larval descriptions based on approximately 350 specimens are given for 12 species of *Chrysops*, 1 *Merycomyia*, 1 *Chlorotabanus*, 1 *Leucotabanus*, and 17 *Tabanus*. Six of the larval descriptions are given for the first time.

Introduction

The present investigation was undertaken to correlate tabanid ecological associations and distribution with the adult and larval taxonomy. Much of the early work on the Tabanidae involved adult taxonomy, and considerably less was done on larval taxonomy or the association of species with ecological habitats. Marchand (1920) gives a summary of the literature on immature tabanids up to that time. Many of the larval investigations published since Marchand's work have dealt with only a few species and in most cases give either limited or no larval descriptions. Notable exceptions are the works of Cameron (1926) and Stone (1930). Hennig (1952) reviewed the world literature and gave a listing of the species for which descriptions of the immature stages had been published. Teskey's (1969) work is the most comprehensive taxonomic treatise on the immature stages and includes complete descriptions, biological information, and literature references for 81 North American species.

Relatively few taxonomic accounts of the Louisiana Tabanidae have been published. The work of Hine (1906, 1907a) included keys and descriptions for 40 species of adults with some biological information included for most species. Jones and Bradley (1923, 1924) listed 55 species as occurring in Louisiana and described the larval habitats of 19. Wilson and Burns (1964) included 60 species in a list of the Louisiana tabanids.

In the present study, the distribution of the Louisiana Tabanidae is correlated with six major vegetational regions which are defined primarily by characteristic plant species. It should be pointed out that not all areas were sampled with the same intensity, and the collecting data in some cases may not reflect the actual distribution of species throughout the state. Twelve genera and 100 species and subspecies are recorded as occurring in Louisiana. A new species of *Chrysops* is described, and changes in the taxonomic status are included for four species. The descriptions for the larvae of 33 species are presented, 11 of which were not included in Teskey's (1969) publication, but 4 of the 11 were given in an unpublished dissertation (Goodwin, 1967). In approximately one-third of the species common to both the present work (southern U.S.) and that of Dr. Teskey (northeastern U.S. and eastern Canada), geographic variation was noted. Consideration of such variation should be made when keying larvae from different regions. Keys, distributional data, and ecological information are included for both adults and larvae.

Economic Aspects

The tabanids, commonly known as horse flies and deer flies, long have been recognized as important pests of man and other animals. When certain species are especially abundant, as in some coastal regions, man's outdoor activities may be seriously hampered. Harassment of livestock by tabanids may result in blood and weight loss and a corresponding decrease in meat and milk production.

In North America the mechanical transmission by tabanids of anaplasmosis, anthrax, equine infectious anemia, equine encephalomyelitis, and tularemia is documented by Anthony (1962) and Jones and Anthony (1964). More recently, the isolation of serotypes of California encephalitis from tabanids (Defoliart, et al., 1969), (Wright, et al., 1970), and the mechanical transmission of hog cholera virus by tabanids (Tidwell, et al., 1972) have been reported. The characteristic nature of tabanid feeding with

repeated probings and frequent moves to another host if disturbed, make them potential mechanical vectors for many disease organisms.

Biological transmission of a disease organism by North American tabanids has been demonstrated by Hibler, et al. (1969, 1970, 1971) who found that certain species of *Hybomitra* and *Tabanus* are natural intermediate hosts for *Elaeophora schneideri* Wehr and Dikmans, a filarioid parasite of elk, deer, and domestic sheep. They indicated that elaeophorosis may possibly be the most important factor responsible for the high annual mortality of elk in certain regions of the Southwest.

Life History

Female tabanids deposit their eggs singly in masses containing from 50 to 700 eggs. Depending on the species, masses may be composed of from one to several tiers and vary in color, shape, and size (generally 5 to 25 mm or more long and 2 to 10 mm wide). The females of many species exhibit oviposition site preferences, but in general the eggs are deposited on vegetation or other structures over water or moist soils. Most tabanids for which information is available breed in aquatic or semiaquatic habitats; however as research continues the list of species that breed in terrestrial habitats is increasing.

The eggs hatch generally in 5 to 8 days, and the larvae drop into the water or soil. Larval development may take a year or more although certain individuals of some species may reach the adult stage in less than 6 weeks. As the larvae complete their development, those in aquatic situations move to higher and drier areas for pupation, and, like those in terrestrial habitats, locate near the surface of the soil. A prepupal period lasting for at least 24 hours is usually characterized by the partial retraction of the head into the prothorax, protrusion of the prothoracic spiracles, and the body becoming somewhat rigid with a corresponding decrease in movement. The pupal period varies from 5 to 10 days (most *Chrysops*) to 3 weeks or more for some of the larger *Tabanus*.

Emergence from the pupal case may last several minutes and within an hour the adult may be capable of moderate flight. Mating probably occurs within 2 to 4 days, and for those females requiring a blood meal for egg development, a host is sought. A wide variety of animals may serve as natural hosts including most large mammals, certain reptiles and birds. Five to 10 days following a blood meal the female deposits a mass of eggs. A single female may oviposit several times during her life span. For sustenance, males, as well as females, feed on nectar or various plant juices and honeydew secretions of other insects.

In Louisiana, a few species are on the wing by the middle of March, but the period of greatest abundance usually extends from mid-May through the first part of July. A general reduction of the composite tabanid population occurs during late July and most of August. An upswing in the population is evident during late August through mid-September due in part to the increased appearance of some late season species as well as a second peak for certain other species.

Ecological Aspects

The area of Louisiana is approximately 48,000 square miles. Located in the Gulf Coastal Plain, it varies little in relief, with the highest elevation 535 feet. The climate is humid subtropical, with the average annual temperatures of the southern and northern portions, 68° and 65°F, respectively. The mean annual precipitation varies from 60 inches in the Southeast to 48 inches in the extreme Northwest. The number of frost free days (growing season) varies from 350 at the extreme southeastern tip to 230 in the northern regions. For additional geographic information concerning Louisiana, the reader is referred to Kniffen (1968).

The Tabanidae of Louisiana were examined in relation to six major vegetational regions modified from Brown (1945). While the delineation of the vegetational regions is broad, it should be pointed out that small disjunct or continuous areas of one region may occur within another when local conditions permit. For example, river-bottom hardwoods associated with the principal drainage systems are found throughout other vegetational regions. Therefore, the association of a specific tabanid fauna with

TABLE 1. Summary of tabanid ecological data.

Species	Mixed bottomland hardwood region	Upland hardwood region	Mixed pine-hardwood region	Longleaf-slash pine or longleaf pine region	Coastal marsh region	Prairie region
Merycomyia						
whitneyi				X		
Silvius						
quadrivittatus		XX				
Chrysops						
abatus				XX		
amazon hubbelli				X		
atlanticus				X	XX	
beameri			X			
bistellatus			XX	XX		
brimleyi		X	XX	XX		
brunneus				XX	XX	
callidus	XX	XX	XX	XX		XX
carbonarius		X	X	X		
celatus				X		
cincticornis			X	X		
cursim				X		
dacne		X		X		
dimmocki	XX			X	X	X
flavidus	XX	XX	XX	XX	XX	XX
fulvistigma			XX	XX		
geminatus geminatus			X	X		
geminatus impunctus		X				
harmani			X			
macquarti		XX	X	XX		
mocchus		X	XX	XX		
montanus			XX	XX		
niger	X	X		X		
nigribimbo				X		
obsoletus lugens				XX		
parvulus			X	X		
pikei	XX	XX	XX	XX		
pudicus			X	X		
reicherti	XX	XX	XX	XX	XX	XX
univittatus				X		
upsilon	XX		XX	XX		
vittatus	XX	XX	XX	XX		
Diachlorus						
ferrugatus	XX			X	X	
Stenotabanus						
magnicallus					X	
Chlorotabanus						
crepuscularis	XX	X	X	X		X
Whitneyomyia						
beatifica	X		X	X		
Leucotabanus						
annulatus	XX	XX	XX	XX		X
Tabanus						
abdominalis	X					
acutus				X	XX	
americanus	XX	X	X	X	X	

Table 1. (*Continued*)

Species	Mixed bottomland hardwood region	Upland hardwood region	Mixed pine-hardwood region	Longleaf-slash pine or longleaf pine region	Coastal marsh region	Prairie region
aranti			X	X		
atratus	XX	X	X	X	X	X
calens	X		X			
coarctatus		X		X		
colon				X		
cymatophorus	X					
eadsi					X	
equalis	X	X	X			
fairchildi			X	X		
fulvulus		X	X	X		
fuscicostatus	XX		X	X	X	
imitans				X		
lineola lineola	XX	XX	XX	XX	X	XX
lineola linellus				X	XX	
longiusculus				X		
maculipennis	XX			X		
melanocerus	XX	XX	XX	XX		X
moderator			X	X		
molestus	XX	XX	XX	XX		
mularis	XX	X	X	X		X
nefarius	X					
nigripes	XX		X	X		
nigrovittatus	X			X	XX	
pallidescens	XX	XX	XX	XX		X
petiolatus	XX	XX	XX	XX		X
proximus	XX		X			
pumilus	XX	X	XX	XX		
quaesitus			X	X		
reinwardti			X	X		
rufofrater				X		
sparus milleri		X	X	X		
stygius	X				X	
sublongus				X		
subsimilis	XX	X	X	X	X	X
sulcifrons	XX	XX	XX	X		X
texanus					XX	
trimaculatus	XX	XX	XX	XX		XX
turbidus	XX	XX	X			
venustus	X		X			X
wilsoni	XX	X				
zythicolor			X			
Hybomitra						
cincta				X		
difficilis		X				
lasiophthalma	XX	X	X			
trispila	X			X		
Agkistrocerus						
megerlei				X		
Hamatabanus						
annularis			X			
carolinensis			X	X		

X infrequently collected
XX commonly collected

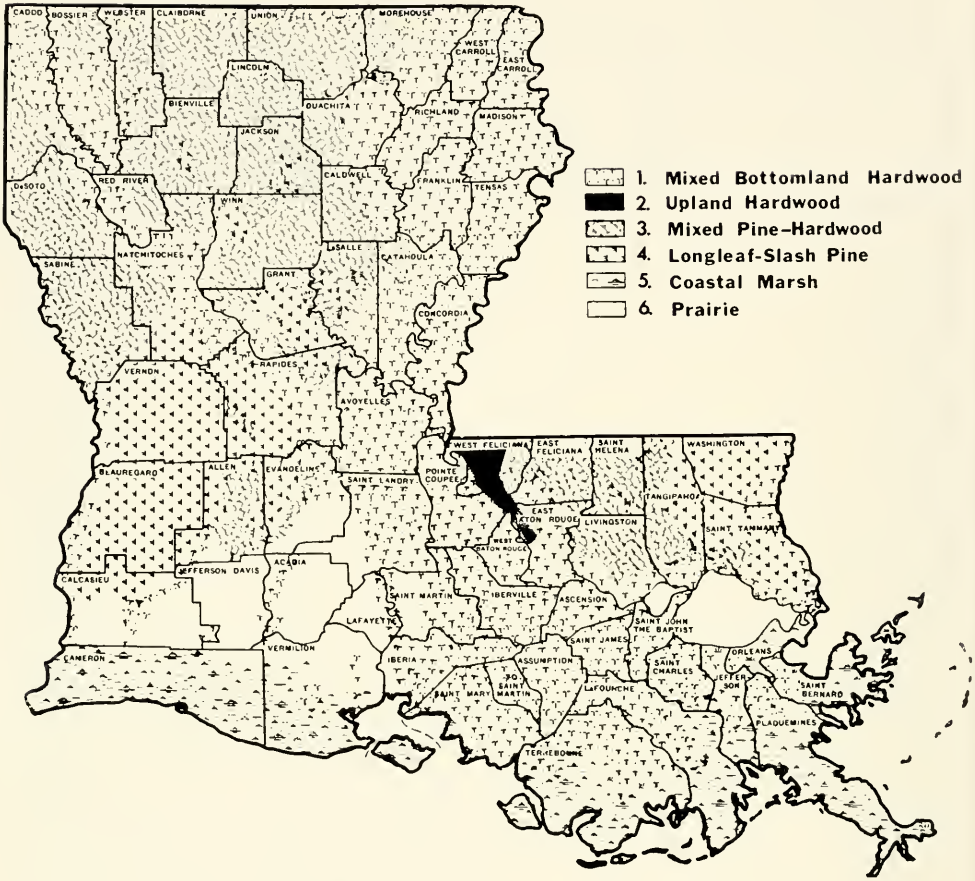


Figure 1. Major vegetational regions of Louisiana.

any given vegetational region must be made with caution. Also, species characteristically found in one vegetational region may frequently overlap with species occurring in other areas. The relative numbers of specimens obtained from the different regions will usually indicate the primary ecological habitat. Many tabanid species, however, are not limited to a particular vegetational region and may be found equally numerous in several of these major areas (Table 1).

Man has played a major role in changing the ecology of the vegetational regions. The development of flood control programs with construction of levees and drainage ditches as well as clearing and drainage of forest lands has had, no doubt, some influence on the tabanid fauna. Of the six species listed by Jones and Bradley (1923, 1924) as serious livestock pests in the vicinity of Baton Rouge, only three, *Tabanus fuscicostatus* Hine, *T. lineola* Fabr., and *Chrysops vittatus* Wied. were commonly collected from this area during the present investigation. Only the two *Tabanus* species could probably be regarded as serious livestock pests.

The principal function of defining vegetational regions is to promote understanding of some basic relationships of tabanids to their environment. The six major vegetational divisions used in this investigation are described below (Fig. 1).

1. Mixed Bottomland Hardwood Region

These forests are associated with the Mississippi floodplain and in lesser degree with the floodplains of the Red, the Atchafalaya,

the Tensas, and other smaller rivers of the state. The bottomlands contain lakes, sloughs, backwater swamps, natural levees, and slopes.

The vegetation bordering the waterways is correlated with the soil type and drainage. Cypress, *Taxodium distichum* Rich., and water tupelo, *Nyssa aquatica* L., swamps which are either permanently or periodically inundated, make up a considerable percentage of the total forest area. Characteristic of the swamp edges are natural levees and higher ridges which support American elm, *Ulmus americana* L.; Nuttall oak, *Quercus nuttallii* Palmer; red maple, *Acer rubrum* L., and other associated types. Soils poorly drained, yet generally free of standing water may have growths of sweetgum, *Liquidambar styraciflua* L.; overcup oak, *Quercus lyrata* Walt.; water hickory, *Carya aquatica* (Michx. f.) Nutt., and other hardwoods. The batture land, which receives periodic inundations, harbors a cottonwood-willow complex.

2. Upland Hardwood Region

This forest type occurs primarily in West Feliciana and East Baton Rouge parishes, but smaller and more localized areas may be found widely distributed throughout much of the state. These regions are characterized by rolling hills and the presence of white ash, *Fraxinus americana* L.; cherrybark oak, *Quercus pagoda* Raf.; Shumard red oak, *Q. shumardii* Buckley; cucumber tree, *Magnolia acuminata* L.; sugar maple, *Acer saccharum* Marsh.; and yellow poplar, *Liriodendron tulipifera* L. Other associated vegetation includes American holly, *Ilex opaca* Ait.; beech, *Fagus grandifolia* var. *caroliniana* Fern. & Rehd.; ironwood, *Carpinus caroliniana* Walt.; magnolia, *Magnolia grandiflora* L.; basswood, *Tilia caroliniana* Miller; white oak, *Q. alba* L.; black cherry, *Prunus serotina* Ehrh.; and silverbell, *Halesia diptera* Ellis.

3. Mixed Pine-Hardwood Region

These forests are associated primarily with the northwestern Louisiana uplands. Smaller areas of this forest type are found in Tangipahoa, St. Helena, Livingston, and East and West Feliciana parishes. These upland regions are characterized by gently rolling hills having permeable subsoils. For the most part, they contain shortleaf, *Pinus echinata* Mill., and loblolly pine, *P. taeda* L., and various hardwoods including southern red oak, *Quercus falcata* Michx.; blackjack oak, *Q. marilandica* Muenchh; cow oak, *Q. michauxii* Nutt.; post oak, *Q. stellata* Wang; and sugar maple, *Acer saccharum* Marsh. Other associated vegetation includes yaupon, *Ilex vomitoria* Ait.; ironwood, *Carpinus caroliniana* Walt.; blackgum, *Nyssa sylvatica* Marsh.; black cherry, *Prunus serotina* Ehrh.; Carolina beech, *Fagus grandifolia* var. *caroliniana* Fern. and Rehd.; dogwood, *Cornus* sp.; and various hickories, *Carya* spp.

4. Longleaf-Slash Pine or Longleaf Pine Region

These forests occur in the eastern area of the state in Washington Parish and in portions of Tangipahoa and St. Tammany parishes. A longleaf pine region also occurs in the mid- and southwestern areas of the state, covering major portions of Vernon, Beauregard, Allen, Grant, and Rapides parishes, as well as lesser portions of adjacent parishes.

The soils of the eastern region are more fertile and support a different, denser, second-growth forest. In the eastern flatwoods, there are extensive stands of slash, *Pinus elliottii* Engelm., and longleaf pine, *P. palustris* Mill., and lesser growths of shortleaf, *P. echinata* Mill., and spruce pine, *P. glabra* Walt. Myriad small sloughs drain the flatwoods and support such hardwood species as redbay, *Persea borbonia* (L.); Allegheny chinkapin, *Castanea pumila* Mill.; mayhaw, *Crataegus opaca* Hook. and Arn.; eastern hophornbeam, *Ostrya virginiana* (Mill.) Koch.; swamp blackgum, *Nyssa sylvatica* var. *biflora* (Walt.) Sarg.; sweetbay, *Magnolia virginiana* L.; and green ash, *Fraxinus pennsylvanica* var. *lanceolata* (Borkh.) Sarg.

In the western region, much of what was once a solid stand of longleaf pine has been cleared and is utilized for pasture. Much of this land is interlaced by streamlets known as "bay galls" and consists of hardwoods characteristically associated with stream bottoms. The longleaf pine flatwoods of southwestern Louisiana differ from those of the east most strikingly by the absence of slash pine.

5. Coastal Marsh Region

The coastal marsh is an area of over four million acres bordering the Gulf of Mexico. Farmlands and forests are negligible in this region, the latter being chiefly composed of cypress, *Taxodium distichum* Rich.; water tupelo, *Nyssa aquatica* L.; buttonbush, *Cephalanthus occidentalis* L.; black willow, *Salix nigra* Marsh.; and associated wet-land hardwoods. Throughout the salt marsh there are natural levees and ridges which support live oak, *Quercus virginiana* Mill.; hackberry, *Celtis laevigata* Willd.; marsh-elder, *Iva frutescens* L.; swampbay, *Persea palustris* (Raf.) Sarg., and other vegetation.

The coastal marshlands may be divided into a series of gradually increasing salinities from the inner freshwater region to the salt water of the Gulf. The principal vegetation from the fresh to the salt water areas is cattail, *Typha* sp.; cutgrass, *Zizaniopsis miliacea* (Michx.) Doell & Aschers; bulrush, *Scirpus robustus* Pursh.; saw grass, *Mariscus jamaicense* Crantz; couch grass, *Spartina patens* (Ait.); blackrush, *Juncus roemerianus* Scheele; quillcane, *Spartina cynosuriodes* (L.) Roth; salt grass, *Distichlis spicata* (L.) Greene; and salt cane, *Spartina alterniflora* Loisel.

6. Prairie Region

In the southwestern portion of the state, a prairie separates the marsh from the western longleaf pine region. Some typical prairie vegetation includes prairie-beardgrass, *Andropogon scoparius* Michx.; butterwort, *Pinguicula* sp.; false indigo, *Baptisia leucantha* T. & G.; Ruellia, *Ruellia pedunculata* Torr.; and compass-plant, *Silphium laciniatum* L. Forested lands comprise only 18 percent of the land area. These forested lands of typical oak and mixed hardwoods are confined predominantly to stream courses or fringes of the lower swampy areas.

Collecting Methods

Tabanid larvae and adults were collected throughout Louisiana and to a lesser extent in neighboring states. Most larvae were obtained by a search of the marginal areas of ponds and streams, and in swamps, although other habitat types occasionally proved to be suitable for some species of tabanids. Specific habitats examined included terrestrial soils, wet or dried mud, moss, within rhizomes or in plant roots, dead wood, among leaves or other debris, in tree holes, under logs, beneath carrion, and in water.

The immature tabanids were obtained by hand sorting the substratum or by using a wire screen. Small amounts of mud or soil were placed on the screen and gently agitated while submerged in water. The soil was washed away, leaving only the larger pieces of debris and any larvae present. Hand sorting was effective when searching for immature tabanids in materials such as rotten wood or matted leaf litter. A hand cultivator was utilized to rake through large areas of soil and other debris to locate larvae. In general, the depth of examination of soil was less than 20 cm. Soil samples suspected of containing larvae were brought to the laboratory and transferred to Berlese funnels to recover any immatures present.

Adult tabanids were collected with insect nets, in autos and buildings, and by the use of New Jersey light traps, Malaise, and canopy traps, the latter similar to that described by Catts (1970). The Malaise and canopy traps and auto collections were improved with the addition of CO_2, provided by several pieces of dry ice approximately one kg each. *Chrysops* were collected primarily by using an aerial net. Sweep nets were used to collect tabanids from vegetation during the day and at night. Collections were also made from horses and other livestock.

Rearing and Preservation of Immatures

For rearing, the larvae were placed individually in 20 × 55 mm glass vials ¼ filled with 6 mm glass beads. Water was added to cover the bottom of the vials, and screw cap lids were placed loosely on top. Using glass beads rather than natural substratum, the vial could be rinsed of unused or decaying food, and the larva or exuvia could be easily observed.

The larvae were maintained at room temperature and were offered food at least once a week. The *Tabanus* larvae were fed primarily on the semi-aquatic annelid, *Sparganophilis eiseni* Smith; however, most species

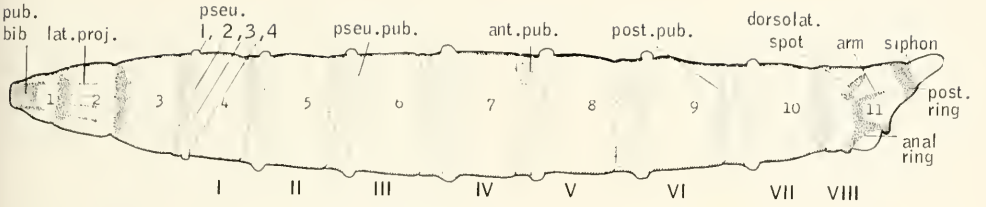


Figure 2. Larva of *Tabanus lincola* showing principal taxonomic characters.

would feed on almost any invertebrate offered, especially if it had been cut up. Liver and raw beef were also consumed by most *Tabanus* larvae. The *Chrysops* larvae seldom consumed the above foods although some fed on small aquatic Chironomidae (Diptera) larvae. Early instar *Chrysops* usually did not survive to complete development.

To facilitate microscopic study, the larvae were immersed in an ice water bath to inhibit movement (Teskey, 1969). Upon pupation, the last larval exuvia was inflated with 70 percent ethyl alcohol using a small syringe and a 27 gauge needle. Injection with alcohol helped to eliminate wrinkles which hindered the observation of diagnostic characters. The larval skin was stored in a vial of 70 percent alcohol. The pupa was placed on damp filter paper until emergence at which time the pupal case was placed with the larval skin, and the adult was allowed to harden before being killed, pinned, and labeled.

Larval Morphology

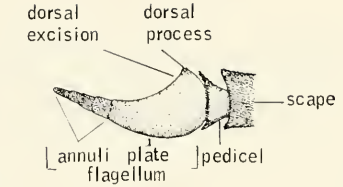
Tabanid larvae are characterized by a cylindrical form, somewhat tapered at both ends (Fig. 2). Full-grown larvae vary in length from 12 mm (small *Chrysops*) to 60 mm or more for large *Tabanus* species. Background color is typically creamy white with light beige to black pubescent patterns. The pubescent patterns are usually similar in over-all appearance but vary in extent, intensity, and configuration for each species.

Pubescence consists of minute spine-like structures, varied in size. Inconspicuous pubescence can best be seen on a section of larval exuvia using a compound microscope at magnifications of 100–430×, but most pubescence is readily observed using a dissecting scope with magnifications of less than 40× and proper lighting. Occasionally, debris may adhere to certain surfaces of the cuticle, giving an appearance of pubescence, and close observation is necessary to distinguish actual pubescent patterns.

Small longitudinal furrows in the cuticular wall are referred to as *striations*. These, when present, may vary from almost imperceptible, broken lines to conspicuous, pronounced longitudinal furrows. Striations are usually closer together on the lateral surfaces of body segments, and when present, more widely spaced on dorsal and ventral surfaces. Finer striae are present at the anterior and posterior margins of segments, and in some species very fine closely spaced striations give a shadowed effect to certain cuticular regions and may be mistaken for fine pubescence. These are found most frequently on the anterior portions of the anal segment and occasionally on the anterior regions of other abdominal segments, and are best observed using magnifications of 100× or greater. The presence or absence of striations and their relative development on different body regions and surfaces may vary among species.

The *head* is an elongated sclerotized capsule, highly movable, and retractable into the thorax. The dorsal surface of the head capsule is composed of a pair of *posterior epicranial plates* fusing anteriorly to form the *epicranium* which extends into a downwardly curved *clypeus*. The clypeus terminates anteriorly at a small upturned *labrum*. Head capsule measurements were made from the labrum to the posterior tip of the epicranial plates. Beneath the epicranial plates and extending beyond them is a pair of internal conspicuous *tentorial rods*, the posterior ends of which are ventrally directed. A detailed description and figures of the head capsule are given by Teskey (1969).

In most species the *thorax* is characterized by the presence of an anterior pubescent



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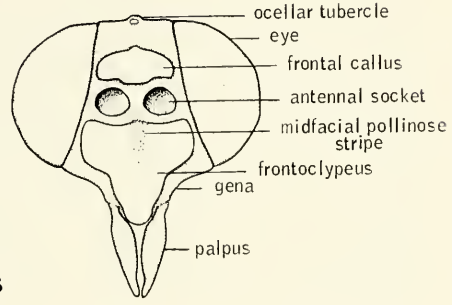

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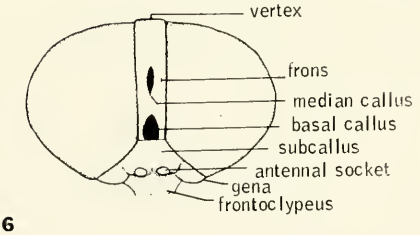

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Figures 3–6. 3, antenna of *Tabanus* (lateral view); 4, antenna of *Chrysops* (lateral view); 5, head of *Chrysops* (frontal view); 6, head of *Tabanus* (frontal view).

band (*annulus*) encircling each of the three segments. A pair of *lateral pubescent projections* (lat. proj.) may extend posteriorly on each side from the prothoracic annulus, and four from each side of the meso- and metathoracic annuli. The presence and extent of development of these projections may vary among species. In some, the area between the lateral prothoracic projections is filled with pubescence and the entire lateral pubescent pattern is referred to as a *bib* (*pub. bib*). Usually, a median ventral pubescent projection is present on the prothorax. In some species pubescence is present on the posterior margins of the meso- and metathorax. The lateral pubescent projections are associated with depressions or grooves in the integument which may appear as closely placed spots. The presence of micro-fine striae in these areas may give the appearance of thin lines of pubescence. When this condition was pronounced, it was figured on the larval drawings for aid in identification. Similar depressions sometimes visible as lateral spots also appear on abdominal segments 1–7.

The *abdomen* is composed of 8 segments, of which all but the last are characterized by the presence of 3 or 4 pairs of anteriorly located fleshy protuberances (*pseudopodia*). These are located dorsally, laterally, ventrolaterally, and ventrally, and are indicated by the numbers 1, 2, 3, 4, respectively (pseu. 1, 2, 3, 4). In those species having only 3 pairs of pseudopodia, the ventrolateral pair is lacking. The *intersegmental line* is located slightly anterior to the pseudopods. The area between this line and the pseudopods may contain pubescence termed *anterior pubescence* (ant. pub.). The pubescence found on and between the pseudopods is termed *pseudopodial pubescence* (pseu. pub.), and that found on the posterior margins of the segments is termed *posterior pubescence* (post. pub.). A gradual decrease in the intensity and extent of the anterior pubescence is found to occur successively from abdominal segments 1 through 7, whereas there is a progressive increase in the amount of posterior pubescence from abdominal segments 1 through 7. The pseudopods bear cuticular spines which may vary considerably from very small near the base of the pseudopod to much larger at the apex. In extreme cases these larger spines may even form well developed crochets.

The *anal segment*, which generally tapers posteriorly, bears a ventral *anal tubercle* and a retractable posterior *respiratory siphon*. The anal tubercle consists of a pair of finely pubescent anal lobes bordered anteriorly and posteriorly by pubescent ridges. The respira-

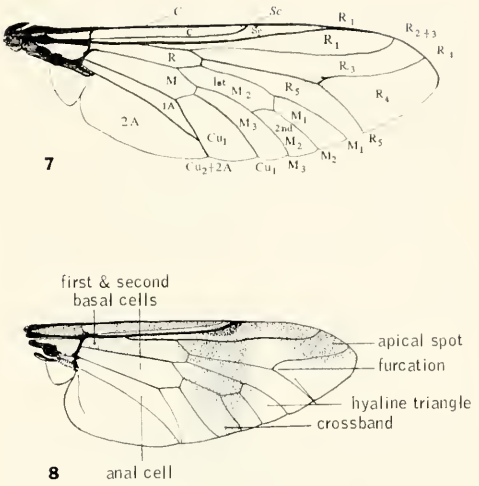
tory siphon varies in length from approximately ½ to several times its basal diameter. In many species, especially of the genus *Chrysops*, a retractable sclerotized *stigmatal spine* extends from the apex of the siphon. A conspicuous lateral pubescent configuration is usually present, as well as a pubescent annulus (*post. ring*) encircling the posterior portion of the segment. In addition, pubescence may be present on other areas. Variation in the extent and configuration of the pubescence on the anal segment is of significant importance in separating species.

Adult Morphology

Problems concerning various species complexes, phenotypic variations, and geographic distribution have often made identification of the adults rather difficult. In certain cases, specimens representing different named species show considerable variation in some key characters. Occasionally, intermediate forms are found that exhibit complete intergradation of these characters. These forms frequently cannot be accurately assigned to either taxon.

The identification of specimens is made primarily by utilizing various cephalic characters and body coloration patterns. In general, tabanids are robust, bristleless flies with hyaline or pictured wings and conspicuous calypteres. The *antennae* are composed of 3 segments; the third (*flagellum*) has a *basal portion* (*plate*) and is divided into 3–8 divisions distally (Figs. 3 & 4). The number of divisions in the 3rd antennal segment is frequently of generic significance, with the basal plate being the 1st division. A dorsal median process or projection may be present on the plate.

The *head* is wide, hemispherical with large *compound eyes*, dichoptic in females and usually holoptic in males. The eyes may bear tiny hairs (pilosity) or be entirely bare. Characteristic eye patterns are present in live specimens of most species; however, the color of this pattern is usually lost when the specimen dries. If the specimen is placed in a humidity chamber the pattern can usually be restored, but the color may be changed. Black, reddish bronze, or gold eye bands in life may appear green, purple, or various shades when viewed from different angles in relaxed specimens.



Figures 7–8. 7, wing of *Tabanus*; 8, wing of *Chrysops*.

In females, the area between the eyes from the top of the head (*vertex*) to the lower inner angle of the eyes is referred to here as the *frons* (Stone, 1938). In some genera the frons is divided by a large oval denuded raised area (*frontal callus*) immediately above the base of the antennae (Fig. 5). Occasionally, at the vertex there is a small, denuded spot (*ocellar tubercle*) which may bear three ocelli in certain groups. In some genera including *Tabanus* (Fig. 6), a denuded line or spot called the *median callus* lies beneath the vertex. Beneath the median callus and occasionally connected to it is a denuded, slightly raised area herein termed *basal callus*. The ventral margin of the basal callus marks the lower extremity of the frons. The *frons ratio* herein refers to the ratio of the frons width (at ventral margin) to the height of the frons (ventral margin to upper inner angle of eye). Above the base of the antennae and below the basal callus is the *subcallus* which may be denuded or pollinose. The *frontoclypeus* lies beneath the antennae and above the oral margin. Lateral to the general region of the clypeus and beneath the eyes lie the *genae*.

Wing veins and cells are labelled using the Comstock-Needham terminology (Fig. 7) and Curran (1934). Wing venation is usually of minor importance as it varies little throughout the family. A term frequently used is *furcation* (*fork*) which

refers to the separation of veins R_4 and R_5. Occasionally a small stump vein may be present or an isolated cloud may surround this area. Wing coloration patterns are especially helpful in separating species of certain genera, e.g., *Chrysops* (Fig. 8).

Abdominal color patterns are also used as diagnostic characters, and descriptions make use of such terms as median triangles, median dorsal stripe, or sublateral spots, the latter referring to lighter areas between the median dorsal line and the lateral margin.

Keys to the Tabanidae

Taxonomic keys are given for the larvae of 8 genera and 35 species of Tabanidae and for 16 genera and 111 species and subspecies of adult Tabanidae. The key to the genera of the larvae occurring in Louisiana and neighboring states is modified in part from Teskey (1969). The keys to the 33 species described in this paper are based on larval specimens collected and reared to the adult stage. Keys to the adults are based in part on those of Jones and Anthony (1964), Philip (1947, 1955), and Stone (1938). These keys were rewritten to include species variations and taxonomic changes. Several species not recorded from Louisiana but reported in neighboring states are included and are denoted by an asterisk (*).

Key to Genera of the Larvae of Tabanidae

1. Body pyriform; integument opaque, roughened; all segments with annular ring of small tubercles or crenulate frills ..... *Goniops chrysocoma* (Osten Sacken)

   Not as above; body cylindrical, somewhat tapered at both ends 2

2. Three pairs of pseudopodia (including dorsal ridge) on each of first five abdominal segments; anal segment hemispherical, ¼ length of preanal segment; mandibles almost straight ..... *Esenbeckia incisuralis* (Say)*

   Pseudopodia present on first seven abdominal segments; differing in other characters 3

3. Larva blackish in appearance (greenish black in living specimens), completely clothed in black, brown, and golden mottled pattern of thick pubescence; mature larva less than 35 mm long (Fig. 24) ..... *Chlorotabanus crepuscularis* (Bequaert)

   Pubescence when present usually limited to anterior and/or posterior margins, pseudopodial pubescence on 1 or more segments; if completely clothed in pubescence, pattern not mottled and mature larva over 40 mm long 4

4. Three pairs of pseudopodia present on each of abdominal segments 1–7; mature larva small, less than 20 mm long ..... *Chrysops* Meigen

   Four pairs of pseudopodia present on abdominal segments 1–7; mature larva usually over 20 mm long 5

5. Siphon composed of two lateral sclerotized plates tapering apically and conspicuous stigmatal spine extending from between plates (Fig. 23) ..... *Merycomyia whitneyi* (Johnson)*

   Siphon lacking sclerotized lateral plates; spine may or may not be present 6

6. Respiratory siphon short, about ½ its basal diameter; rather uniformly-spaced striations encircling all segments 7

   Respiratory siphon longer than ½ its basal diameter; striations, if present on all surfaces, more closely spaced on lateral aspects 8

7. Narrow bands of anterior pubescence encircling at least abdominal segments 1–3; same pubescence not peg-like; mature larva less than 25 mm long (Fig. 25) ..... *Leucotabanus annulatus* (Say)

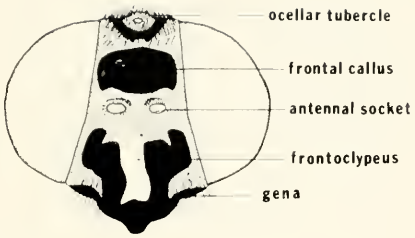
   Anterior pubescence on abdominal segments 1–3 limited to dorso- and ventrolateral bands (incomplete, not encircling segments); pubescence spiney or peg-like in appearance; mature larva over 25 mm long ..... some *Tabanus* Linnaeus

8. Median lateral surfaces of anal segment lacking pubescent markings; striations present on dorsal and ventral surfaces of all abdominal segments ..... *Hybomitra* Enderlein*

Either median lateral surfaces of anal segment with pubescent markings, or striations absent or poorly developed on dorsal and/or ventral surfaces of abdominal segments ..... *Tabanus* Linnaeus

Key to Full-Grown Larvae of Chrysops

1. Respiratory spine absent 2
   Respiratory spine present 5
2. Pubescence of anal segment varying in intensity from extremely pale to light, covering most of anterior aspects; posterior ventrolateral portion largely clear; length of respiratory siphon less than 3 times its basal diameter (Fig. 14) ..... *nigribimbo* Whitney
   Pubescence of anal segment darker, covering posterior ventrolateral portions; clear areas primarily anterior; length of respiratory siphon 3 or more times its basal diameter 3
3. Posterior pubescence of preanal segment with distinct median lateral peak; lateral striations on abdominal segments 2–7 extremely fine, appearing inconspicuous or absent (Fig. 11) ..... *brimleyi* Hine
   Posterior pubescence of preanal segment without median lateral peak; usually small dorso- and ventrolateral peaks present; lateral striations on abdominal segments normal 4
4. Length of respiratory siphon approximately three times its basal diameter; anterior pubescence encircling abdominal segments 1–4 (Fig. 13) ..... *vittatus* Wiedemann
   Length of respiratory siphon approximately four times its basal diameter; anterior pubescence encircling abdominal segment one, absent at least laterally on abdominal segments 2–7 (Fig. 12) ..... *pikei* Whitney
5. Anterior pubescent annulus of prothorax extremely faint, extending ⅔ or more length of segment; lateral pubescent projections absent from all thoracic segments (Fig. 15) ..... *niger* Macquart



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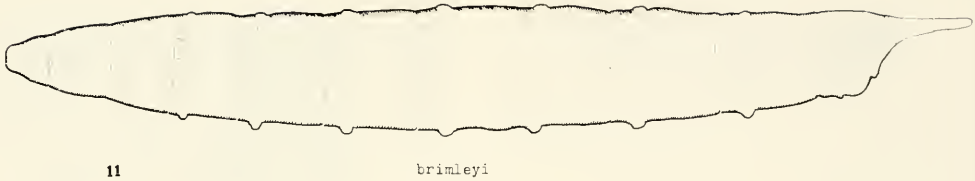
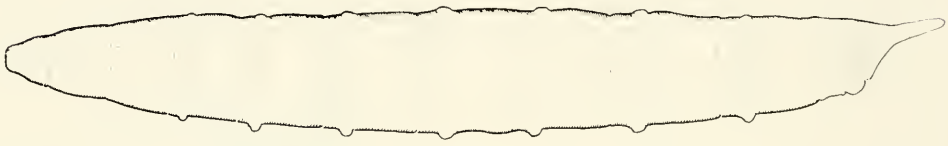
Figures 9–10. *Chrysops harmani* n. sp. female. 9, head (frontal view); 10, dorsal abdominal pattern.

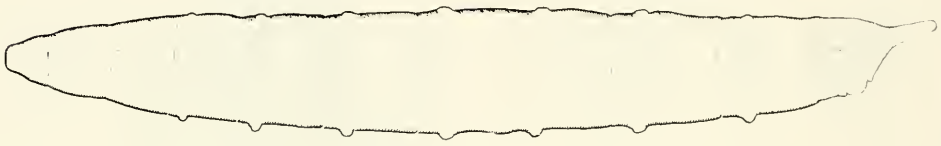
   Anterior pubescent annulus of prothorax narrow, either with paired pubescent projections or lateral bib; lateral projections usually developed at least on mesothorax 6
6. Prothoracic annulus with lateral pubescent bib on each side 7
   Prothoracic annulus with paired lateral pubescent projections on each side 9
7. Mature larva approximately 12–13 mm; posterior pubescent ring of anal segment extending approximately ¼ length of segment dorsally; pubescence somewhat reduced posteriorly before reaching respiratory siphon (Fig. 16) ..... *univittatus* Macquart and *upsilon* Philip



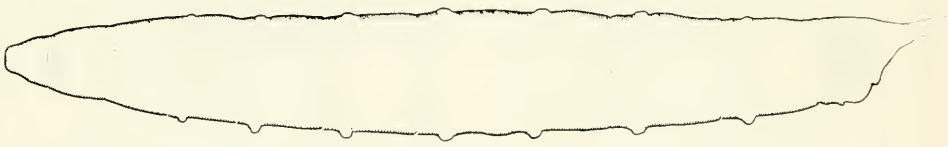
11 brimleyi



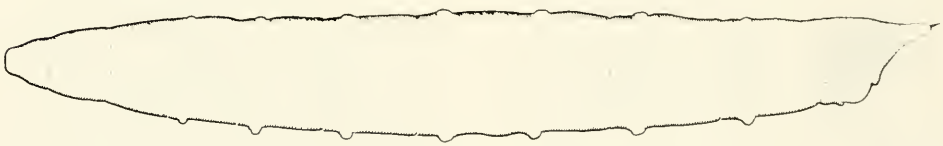
12 pikei



13 vittatus



14 nigribimbo



15 niger

Figures 11–15. Larvae of *Chrysops*.

Mature larva usually over 13 mm long; posterior pubescent ring of anal segment extending approximately ⅔ or greater length of segment dorsally; pubescence continuous to siphon 8

8. Pubescence of anal segment distinct, covering approximately ⅚ or more of segment; posterior pubescence present on abdominal segments six and seven, distinctly encircling the latter (Fig. 17) ..... *celatus* Pechuman

Pubescence of anal segment covering approximately ¾ of segment; posterior pubescence absent on abdominal segment six (Fig. 18) ..... *flavidus* Wiedemann

9. Anal segment with conspicuous isolated pubescent spots located dorsolaterally in anterior clear area; anterior pubescence of abdomen completely encircling only abdominal segments 1–2 (Fig. 22) ..... *cincticornis* Walker

Anal segment without conspicuous dorsolateral isolated pubescent spots; anterior pubescence encircling at least first three abdominal segments 10

10. Posterior pubescence broadly encircling preanal segment (Fig. 20) ..... *dimmocki* Hine

Posterior pubescence absent on preanal segment or limited to small median lateral peak 11

11. Posterior pubescence usually absent on preanal segment; if present, limited to tiny median lateral spot (Fig. 19) ..... *reicherti* Fairchild

Posterior pubescence forming median lateral peak on preanal segment (Fig. 21) ..... *callidus* Osten Sacken

Key to Full-Grown Larvae of Tabanus

1. Respiratory spine present 2

Respiratory spine absent 6

2. Prothoracic annulus with paired lateral pubescent projections on each side 3

Prothoracic annulus with lateral pubescent bib on each side 5

3. Lateral anal arm usually not connected to anal pubescent ring; lateral prothoracic projections usually about two times longer than greatest width (Fig. 34) ..... *aranti* Hays

Lateral anal arm connected to anal pubescent ring; lateral prothoracic projections relatively narrow, usually about 2.5 times longer than greatest width 4

4. Living larva green in color; lateral pubescent projections of mesothorax expanded apically (club-shaped); anterior pubescence present dorsally on anal segment (Fig. 32) ..... *maculipennis* Wiedemann

Larva creamy white; lateral pubescent projections of mesothorax not expanded apically; no anterior dorsal pubescence on anal segment (Fig. 33) ..... *nigrescens* Palisot de Beauvois*

5. Lateral anal arm connected to anal pubescent ring; lateral pubescent projections of mesothorax slightly expanded apically; rather distinct brown pubescence on all segments (Fig. 36) ..... *stygius* Say

Lateral anal arm not connected to anal pubescent ring; mesothoracic projections seldom expanded apically; pubescence light on most segments (Fig. 35) ..... *proximus* Walker

6. Most abdominal pseudopods long and conspicuous with their apices having from 5 to 15 crochets arranged in semicircle; lateral pubescent arm of anal segment not connected to anal ring (Fig. 39) ..... *fairchildi* Stone

Pseudopods normal, without crochets 7

7. Length of respiratory siphon approximately ½ its basal diameter; striations pronounced and rather evenly spaced on all body surfaces (Fig. 26) ..... *molestus* Say

Length of respiratory siphon equal to or greater than its basal diameter 8

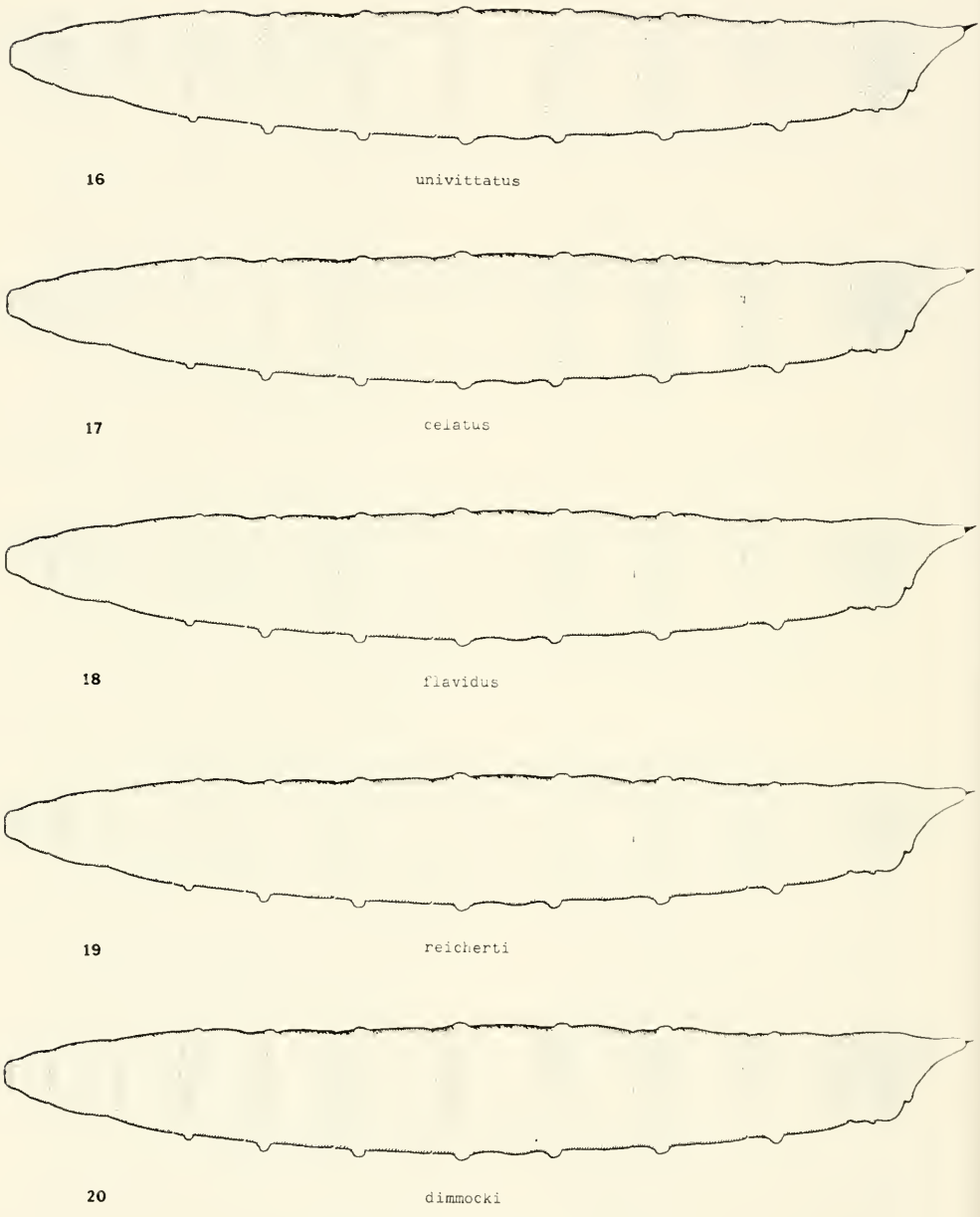
8. Anal segment elongated posteriorly, length of respiratory siphon approximately four times its basal diameter (Fig. 40) ..... *pumilus* Macquart

Anal segment not especially elongated posteriorly, length of respiratory siphon less than 2.5 times its basal diameter 9

9. Pubescence solid, covering entire body surface; large approximately 50 mm long (Fig. 38) ..... *americanus* Forster

Pubescence not entirely covering surface, usually limited to anterior and/or posterior margins of most segments and to pseudopodial pubescence of abdominal segments 1–7 10

10. Pubescence dark and extensive on all



Figures 16–20. Larvae of *Chrysops*.

segments; dorsolateral pubescent bars connect anterior and posterior pubescence on abdominal segments 1–7 (Fig. 37) ..... *atratus* Fabricius

Pubescence not extensive; dorsolateral pubescent bars absent on abdominal segments 1–7 11

11. Prothorax with lateral pubescent bib 12

Prothorax with paired lateral pubescent projections on each side or lateral prothoracic projections absent entirely 14

12. Larva usually 25 mm or less in length; length of respiratory

siphon approximately equal to its basal diameter; lateral pubescent arm of anal segment not reaching posterior pubescent ring (Fig. 2) ..... *lineola* Fabricius

Mature larva over 30 mm in length; respiratory siphon longer than width at base; lateral pubescent arm of anal segment connecting or almost so to pubescent ring ... 13

13. Respiratory siphon about 1.3 times as long as width at base; pubescent arm of anal segment connected to posterior pubescent ring; short lateral posteriorly directed pubescent peak between pseudopods one and two on preanal segment; striations pronounced on dorsal surface of preanal segment (Fig. 31) ..... *reinwardti* Wiedemann

Length of respiratory siphon about twice its basal diameter; pubescent arm of anal segment usually not connected to posterior pubescent ring; no short posteriorly directed pubescent peak between pseudopods one and two on preanal segment; dorsal striations on preanal segment absent or weak (Fig. 30) ..... *trimaculatus* Palisot de Beauvois

14. Faint anterior and posterior pubescence present on abdominal segments 1–7; anterior pubescent annuli of thorax with lateral projections on all segments (Fig. 28) ..... *sulcifrons* Macquart

Anterior and posterior pubescence absent on abdominal segments 1–7; lateral pubescent projections absent at least from meso- and metathoracic segments 15

15. Lateral pubescent arm present to some degree on anal segment (Fig. 29) ..... *melanocerus* Wiedemann and *petiolatus* Hine

Lateral pubescent arm absent on anal segment (Fig. 27) ..... *nigripes* Wiedemann

Key to Genera of Adult Tabanidae

1. Hind tibiae with two apical spurs matching those of middle tibiae (small in *Merycomyia*); three ocelli at vertex 2

Hind tibiae without spurs; no functional ocelli, though tubercle may be present 6

2. Antennae 9–10 segmented (flagellum with at least seven divisions, the basal one not greatly differentiated) 3

Antennae with not over seven segments (flagellum with at most five divisions, the basal one considerably elongated) 4

3. Eyes of female with upper angles sharply acute; wings with wide, sharply marked, irregular brown pattern; cell R_5 broadly open ..... *Goniops* Aldrich

Eyes of female normal; wings of uniform color; cell R_5 petiolate ..... *Esenbeckia* Rondani*

4. Third antennal segment with three divisions (two annuli) ..... *Merycomyia* Hine*

Third antennal segment with five divisions (four annuli) 5

5. Pedicel of antenna about ½ as long as scape; wings usually spotted; eyes speckled ..... *Silvius* Meigen

Pedicel of antenna more than ½ as long as scape; wing usually with dark band; eye with patterned maculations ..... *Chrysops* Meigen

6. Frons of female without callosity; body compact, uniformly greenish yellow in life ..... *Chlorotabanus* Lutz

Frons of female with callosity; color of body not as above 7

7. Third antennal segment with forward-projecting hook-like process above; eye pilose 8

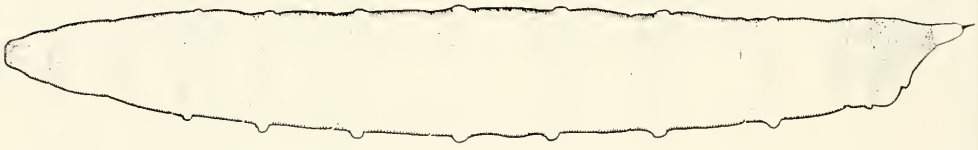
If third antennal segment has forward-projecting process, eye is bare; if eye is hairy, there is no forward projecting process on third antennal segment 9

8. Subcallus with erect black hairs laterally ..... *Agkistrocerus* Philip

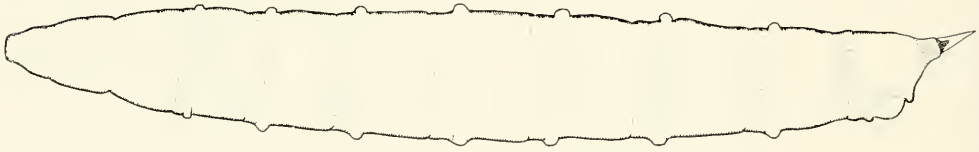
Subcallus without such hairs ..... *Hamatabanus* Philip

9. First antennal segment considerably longer than thick; third antennal segment with four divisions (three annuli); eye in life and wing with

21 callidus



22 cincticornis



23 whitneyi

24 crepuscularis

25 annulatus

Figures 21–22. Larvae of *Chrysops*.
Figure 23. Larva of *Merycomyia*.
Figure 24. Larva of *Chlorotabanus*.
Figure 25. Larva of *Leucotabanus*.

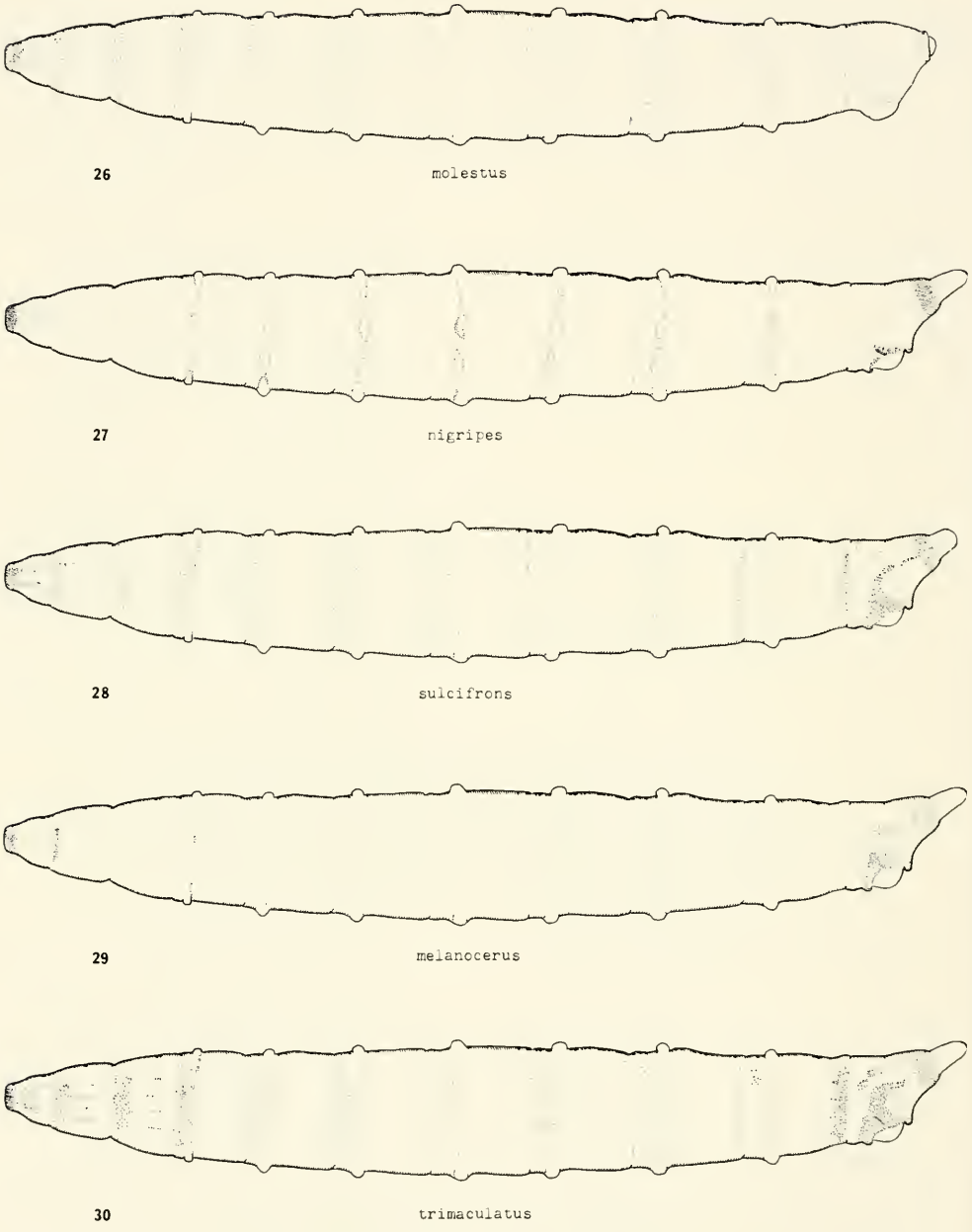
irregular bands and spots ..... *Haematopota* Meigen*

First antennal segment scarcely longer than thick; third antennal segment usually with five divisions (four annuli), if less, then wings hyaline; eye in life with regular bands or unicolorous 10

10. Vertex with distinct ocelligerous tubercle 11
Vertex without such tubercle; if vertex is raised in male, it is pollinose 12
11. Eye ostensibly bare; frons narrow, callosity long and narrow; scutellum pallid ..... *Leucotabanus* Lutz
Eye usually pilose; frons variable in width, basal callus correspondingly broad; scutellum dark ..... *Hybomitra* Enderlein
12. Subcallus very swollen and shiny; genae denuded, shiny; third antennal segment slender; black species; medium sized, 13–16 mm ..... *Whitneyomyia* Bequaert
Not with above combination of characters 13
13. Basicosta bare 14
Basicosta with hairs like those on costal vein 15
14. Frons of female narrow, height seven times width at base, median callus a slender line; wing with at least subapical brown spot ..... *Diachlorus* Osten Sacken
Frons less than six times as high as wide; wing hyaline, usually with stump vein at furcation ..... *Stenotabanus* Lutz
15. Small fly, 7–9 mm; annulate part of third antennal segment with three divisions ..... *Microtabanus* Fairchild*
Annulate part of third antennal segment with five divisions; length of fly variable ..... *Tabanus* Linnaeus

Key to Females of Chrysops

1. Wing entirely hyaline; small black species ..... *hyalinus* Shannon*
Wing infuscated, occasionally faint; if faint, at least face yellowish 2
2. Apex of wing beyond crossband usually hyaline, if trace of infuscation along costa, then submedian areas on first two abdominal tergites yellow 3
Apex of wing beyond crossband infuscated; i.e., apical spot present (narrow in some *brimleyi*) 7
3. Midfacial pollinose stripe beneath antennae ½ to ¾ distance to oral margin 4
No midfacial pollinose stripe (occasionally short stripe less than ⅛ distance to oral margin in *fulvistigma*) 5
4. Cell Cu_1 with basal hyaline lunule ..... *carbonarius* Walker
Cell Cu_1 entirely infuscated basally ..... *cincticornis* Walker
5. Wing picture with crossband saturate and reaching or nearly reaching hind margin, abdomen entirely dark ..... *niger* Macquart
Wing picture dilute, crossband fading well before hind margin or if crossband distinct submedian areas on 1st and 2nd abdominal tergites yellow 6
6. Both basal cells entirely hyaline; abdomen with yellow pattern basally ..... *fulvistigma* Hine
First basal cell dilutely infuscated; abdomen entirely dark ..... *nigribimbo* Whitney
7. Face with distinct median pollinose stripe usually extending ½ or more distance to oral margin; if stripe shorter then abdomen dark with median dorsal yellow stripe 8
Face bare, if stripe present, not extending more than ⅛ distance to oral margin 12
8. Abdomen yellow with black middorsal markings, usually forming solid longitudinal band; terminal segments darker 9
Abdomen otherwise marked 10
9. Fore coxae entirely yellow; apical spot terminating in middle ½ of cell R_4 ..... *dorsovittatus* Hine*
Fore coxae dark; apical spot usually filling all of cell R_4 and occasionally entering cell R_5 ..... *abatus* Philip
10. Abdomen with at least faint trace of yellow middorsally; first basal cell mostly hyaline or with at most only trace of infuscation throughout its length ..... *upsilon* Philip
Abdominal integument entirely black; first basal cell noticeably infuscated although clear window may be present distally 11
11. Both basal cells infuscated except for hyaline windows distally .....



Figures 26–30. Larvae of *Tabanus*.

amazon hubbelli Philip

First basal cell completely infuscated, second basal cell hyaline ..... *separatus* Hine

12. Base of vein R_4 (fork) with isolated spot or this may be extension from cross band (may be faint in *brimleyi*) 13

Fork with no prominent spot though area may be included in apical tinting of wings 14

13. Outer margin of crossband nearly

Key to Females of Chrysops (continued)

straight or gently bowed; apical spot narrow usually just reaching into outer corner of cell R_4 ..... *brimleyi* Hine

Outer margin of crossband usually strongly bowed; apical spot broad and drop-shaped; occasionally hyaline areas faintly infuscated ..... *fuliginosus* Wiedemann*

14. First basal cell completely infuscated, if hyaline spot in apex, it does not plainly cross cell; crossband reaching hind margin 15

First basal cell with at least subapical hyaline spot crossing cell, sometimes cell almost entirely hyaline (in *montanus* spur occasionally reaches apex); crossband not always reaching hind margin 29

15. Entire apex of wing infuscated except for isolated clear spot in cell R_3 above fork ..... *bistellatus* Daecke

Apical wing pattern otherwise 16

16. Wing pattern with usual hyaline areas luteous or tinted; usually yellowish brown species; if black, thorax with conspicuous yellow stripe on each side above wing base 42

Wing pattern in sharper contrast with definite hyaline areas 17

17. Abdomen bicolored, two basal tergites yellow, remainder black ..... *tiduelli* Philip & Jones*

Abdomen otherwise marked 18

18. Apex of hyaline triangle nearly reaching or crossing R_{2+3} and often going beyond (in occasional *parvulus* and *dacne*, hyaline triangle in cell R_3 is only vaguely indicated by reduced subhyaline crescentic margin along crossband) 22

Apex of hyaline triangle seldom reaching much beyond fork 19

19. Apex of hyaline triangle not extending beyond vein M_1 (rarely hyaline triangle extending into cell R_5, see variations) ..... *moechus* Osten Sacken

Apex of hyaline triangle extending beyond vein M_1 20

20. Abdomen with two submedian dark lines usually expanding posteriorly ..... *macquarti* Philip

Abdomen quadristriate 21

21. Frontal callosity and scutellum yellow ..... *vittatus* Wiedemann

Frontal callosity and scutellum predominantly dark ..... *striatus* Osten Sacken

22. Frontal callosity yellow often with brown upper margin 23

Frontal callosity black or occasionally with brown shades 24

23. Hyaline triangle with wide base on hind margin behind cell R_4; crossband usually not invading cell Cu_1 ..... *beameri* Brennan

Hyaline triangle very narrow, more crescentic, apical spot usually invading cell M_1, crossband often crossing cell Cu_1 as lighter shadow ..... *hinei* Daecke*

24. Abdomen yellow with either single median longitudinal black band or two prominent submedian black stripes; two sublateral stripes usually present on tergites 3–5 25

Abdomen otherwise marked 26

25. Abdomen with single median longitudinal black band; first basal cell lightly infuscated; apical spot fading in cell R_4 ..... **harmani** n. sp.

Abdomen with two submedian black stripes; first basal cell saturate, same color as crossband; apical spot extensive, filling all of cell R_4 and occasionally entering apex of M_1 ..... *pikei* Whitney

26. Abdomen yellow with four black stripes ..... *sequax* Williston

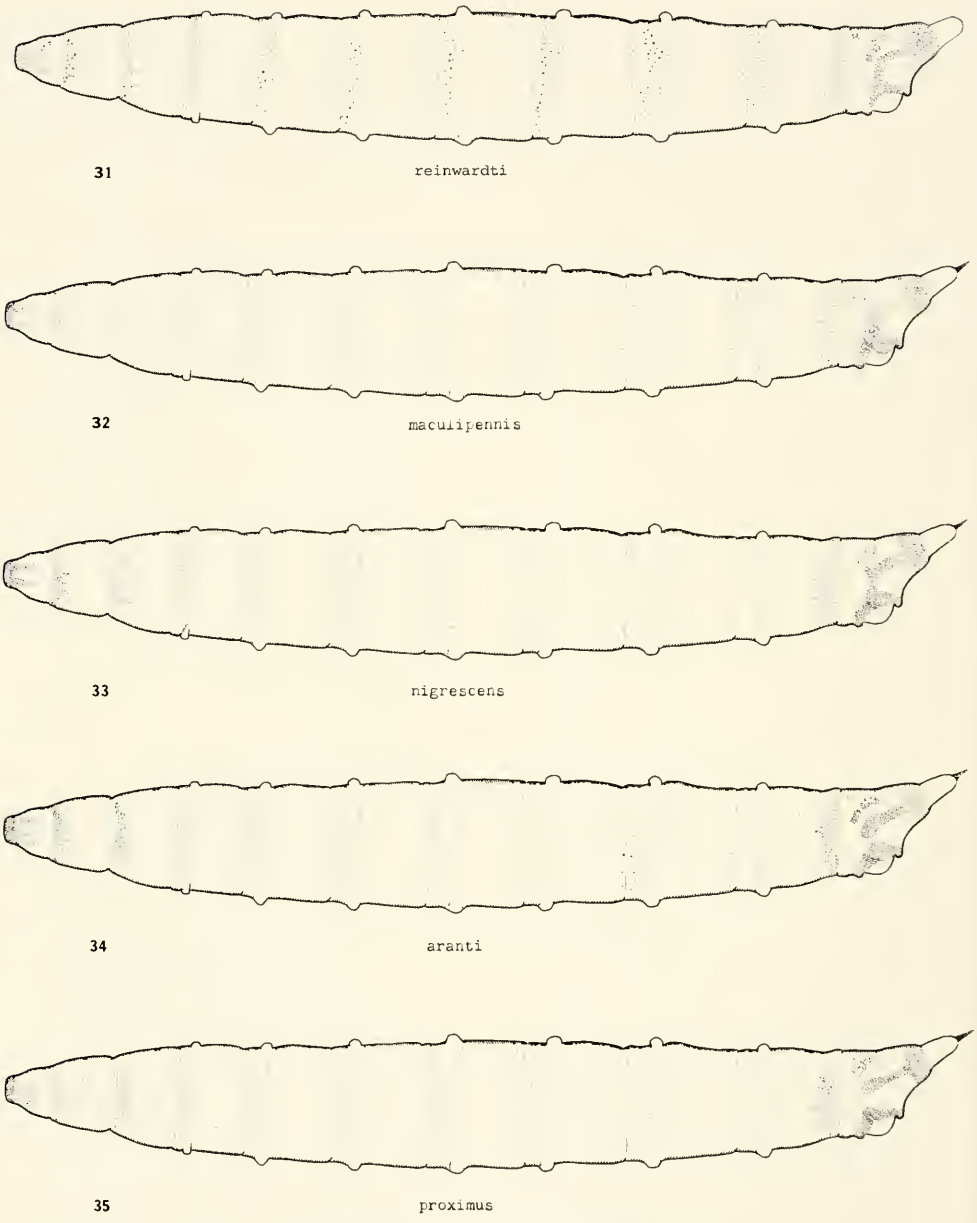
Abdomen otherwise marked 27

27. Thorax with conspicuous yellow stripe on each side above wing base 43

Thoracic bands confined to pleura 28

28. Hind legs predominantly yellowish to brown; abdomen usually with at least suggestions of one or three gray or yellowish stripes; apical spot crossing into cell R_5 at least as shadow ..... *dacne* Philip

Hind legs predominantly fuscous; abdomen dark, seldom with obscure pattern on tergite two;



Figures 31–35. Larvae of *Tabanus*.

apical spot usually fading in cell R_4 ..... *parvulus* Daecke

29. Apical spot just wider than cell R_1 at its origin and only exceptionally expanded distally; about ⅓ and ¼ of respective two basal cells infuscated; crossband fading well before hind margin; frontal callosity customarily yellow with brown upper margin rounded and almost as tall as broad; tergites one and two yellow with connected, sharp black hourglass-shaped spot; sternites two and

Key to Females of Chrysops (continued)

three with sublateral spots ..... *sackeni* Hine*
Without this combination of characters 30

30. Abdomen quadristriate or quadrivittate, usually with median inverted "V" on tergite two; apical spot drop-shaped, usually filling at least ½ of cell R_4, apex of hyaline triangle often reaching or even slightly crossing vein R_{2+3} ..... *montanus* Osten Sacken
Without this combination of characters 31

31. Apex of hyaline triangle clearly reaching or crossing vein R_{2+3}; first basal cell infuscated to about ½ or less than ½ its length 32
Apex of hyaline triangle not reaching vein R_{2+3} 37

32. Apical spot narrow, seldom widened apically; cell Cu_1 partially infuscated; hind femora black ..... *callidus* Osten Sacken
Apical spot widened beyond its origin, drop-shaped and usually extending into more than just apex of cell R_4; if apical spot narrow then cell Cu_1 mostly clear; hind femora variable in color 33

33. Abdomen predominantly blackish with long middorsal yellow stripe attenuated caudally, sometimes with abbreviated stripes on either side ..... *univittatus* Macquart
Abdomen predominantly yellow and otherwise patterned 34

34. Apical spot practically or quite separated from crossband by apex of hyaline triangle and occupying nearly whole of cell R_4; crossband at least filling cell M_3 to margin 35
Apical spot joined to crossband by about width of cell R_1 36

35. Second abdominal segment with two submedian dark dashes ..... *geminatus geminatus* Wiedemann
Second abdominal segment entirely yellow ..... *geminatus impunctus* Krober

36. Hind femora yellow; median spot on tergite one inconspicuous or very reduced; crossband may be dilute or saturate ..... *cursim* Whitney
Hind femora dark; conspicuous spot beneath scutellum on tergite one; crossband saturate; (occasional *dimmocki*, see couplet 38) ..... *pudicus* Osten Sacken

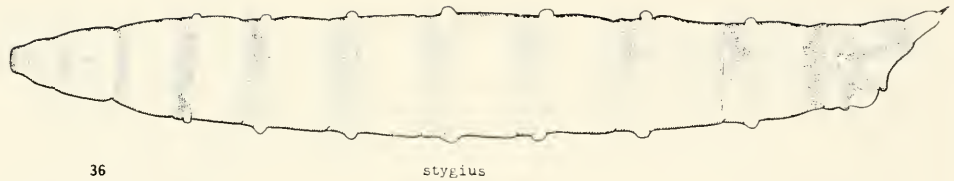
37. Apical spot extending along whole hind margin of wing enclosing pronounced contrasting subhyaline streak (sickle) along outer border of crossband; scapes strongly swollen; callus yellow; frontal callosity protuberant; body rich brownish with indefinite abdominal pattern ..... *brunneus* Hine
Without this combination of characters 38

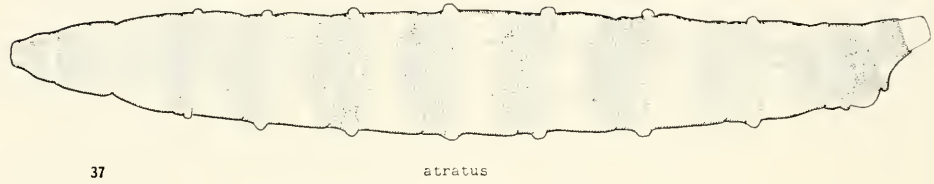
38. Inverted "V" on tergite two tall, black, completely crossing tergite; hind femora and tibiae usually brown to black; frontal callus usually black ..... *dimmocki* Hine
Inverted "V" usually flattened, brownish, only occasionally attaining anterior margin; frontal callus yellow; usually hind femora and tibiae predominantly yellow 39

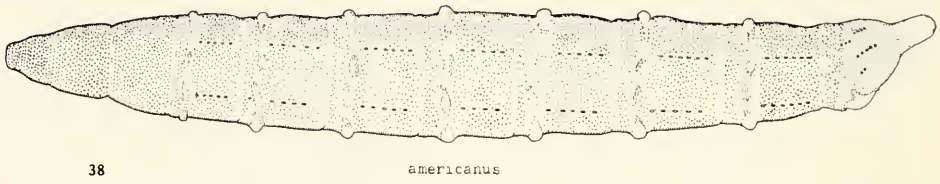
39. Wing pattern not sharply outlined, usual hyaline areas tinted; scapes moderately swollen but not to extent in *brunneus*; mesonotum typically grayish green with dark stripes (coastal species) ..... *atlanticus* Pechuman
Wing pattern distinctly outlined or if usual hyaline areas slightly tinted then anterior ½ of second tergite pale translucent yellow; scapes of antennae but little swollen 40

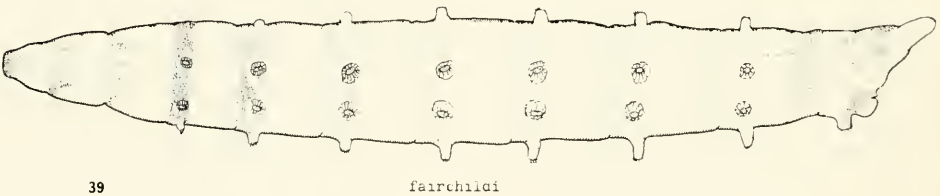
40. Thorax typically yellowish with brown stripes; outer margins of crossband usually rather straight; inverted brown "V" on tergite two not especially flattened, sides of this tergite brownish yellow ..... *flavidus* Wiedemann
Differing in one or more of these characters 41

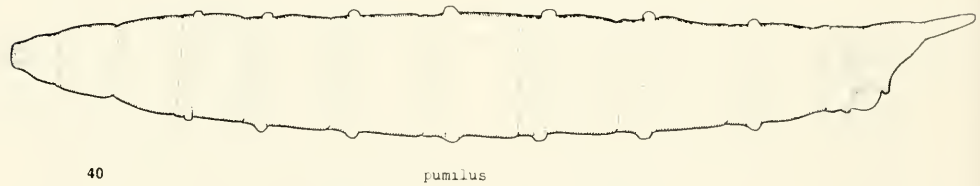
41. Tergite two with median "V" flattened to about ½ the length of tergite leaving anterior "collar" of pale translucent yellow; thorax











Figures 36–40. Larvae of *Tabanus*.

with yellow and brown stripes ..... *reicherti* Fairchild

Tergite two not as above; thorax grayish green with fuscous stripes ..... *celatus* Pechuman

42. Mostly black species 43
Yellowish brown species 44

43. Abdominal pattern usually consisting of three yellowish stripes, sometimes obsolescent laterally ..... *obsoletus* Wiedemann

Abdomen dark, without pattern or only trace of median yellow stripe ..... *obsoletus lugens* Wiedemann

44. Apical spot extending along whole hind margin of wing enclosing pronounced contrasting subhyaline streak (sickle) along outer

border of crossband; mesonotum yellowish with dark brown stripes; scapes strongly swollen ..... *brunneus* Hine

Subhyaline streak beyond crossband, if present, not pronounced; mesonotum grayish green with dark stripes; scapes moderately swollen ..... *atlanticus* Pechuman

Key to Males of Chrysops (excluding *abatus, amazon hubbelli, bistellatus, harmani,* and *tidwelli*).

1. Wing hyaline, at most only trace of infuscation; palpi black; small black species ..... *hyalinus* Shannon*
   Wing infuscated to varying degree, if faint and species black, then face and palpi with yellow 2
2. Apex of wing beyond crossband hyaline, at most occasional indefinite trace of infuscation along costa 3
   Apical spot present and distinct 7
3. Wing picture saturate, infuscated and hyaline areas contrasting 4
   Wing picture dilute (crossband distinct in occasional specimen of *fulvistigma*) 6
4. Frontoclypeus yellow with black lateral facial calli; midfacial pollinose stripe absent or reduced to small peg-like projection; apical portion of first and second basal cells usually partially hyaline; clear area in apex of second basal cell occasionally extending into base of cell Cu_1 ..... *niger* Macquart
   Frontoclypeus black with midfacial pollinose stripe that extends at least ½ the distance to oral margin; apical portion of first and second basal cells completely hyaline 5
5. Well defined clear lunule in base of cell Cu_1 ..... *carbonarius* Walker
   Cell Cu_1 without basal clear lunule ..... *cincticornis* Walker
6. Abdomen and first basal cell entirely dark brown to black ..... *nigribimbo* Whitney
   Abdomen with basal yellow patterns; first basal cell not infuscated ..... *fulvistigma* Hine
7. Entirely black; apical spot distinctly separated from crossband; both basal cells infuscated ..... *separatus* Hine
   Not as above 8
8. Abdomen yellowish with contrasting middorsal black stripe; distinct midfacial pollinose stripe ..... *dorsovittatus* Hine*
   Not as above 9
9. Midfacial pollinose stripe present and lateral facial calli often protuberant; apical spot broad including cell R_4 10
   Midface bare, or abbreviated spur on usually less than upper ⅓ of face; facial calli only exceptionally protuberant; apical spot variable 12
10. Apex of hyaline triangle exceeding vein R_{2+3}; prominent midfacial pollinose stripe ..... *upsilon* Philip
    Apex of hyaline triangle seldom extending much beyond fork; midfacial pollinose stripe reduced to very thin broken line or represented by short stump that extends approximately ⅓ or less distance to oral margin 11
11. Midfacial pollinose stripe very thin, extending most of distance to oral margin; facial pollinosity yellow; occasionally trace of yellow median line on abdominal dorsum ..... *dacne* Philip
    Midfacial pollinose stripe extending less than ⅓ distance to oral margins; facial pollinosity gray; abdomen entirely black ..... *parvulus* Daecke
12. Whole apical area of wing smoky, enclosing hyaline triangle; usually wing pattern dilute and indefinite; second basal cell often extensively hyaline (some *cursim, pudicus,* and *celatus* with very faint wing infuscation, see couplet 27) 13
    Wing pattern normally saturate, sharp and contrasting with definite apical spot although latter may occasionally be contiguous with faint infuscation in hyaline areas along posterior wing margin 18

Key to Males of Chrysops (continued)

13. Primarily dark species; frontoclypeus pale yellow with dark brown or black facial calli and gena 14
Yellow or tan species; entire face bright yellow 16
14. Yellow stripe on each side of thorax above wing base 35
Thorax darker, not as above 15
15. Scape, fore coxa, femur, yellow to brown; pleura with obvious plumbeous stripes ..... *parvulus* Daecke
Scape, fore coxa, femur, black; faint stripes on pleura ..... *fuliginosus* Wiedemann*
16. Basal ½ of tergite two pale translucent yellow ..... *reicherti* Fairchild
Basal ½ of tergite two straw yellow to brownish yellow 17
17. Robust scapes; median series of indefinite geminate spots on abdomen; indefinite infuscated wing pattern although crossband and apical spot may be somewhat darker ..... *atlanticus* Pechuman
Distinctively swollen scapes; indefinite abdominal pattern; wing pattern distinct, pronounced enclosed hyaline sickle or window beyond crossband ..... *brunneus* Hine
18. Apical spot widened including practically all of cell R_4, often invading cell R_5 (occasional *univittatus* with cell R_4 infuscated, see couplet 23) 30
Apical spot seldom reaching beyond ½ of cell R_4 19
19. Apical spot relatively slender, hardly widened beyond its juncture with crossband and reaching narrowly into apex of cell R_4; dark brown to black hind femora; at least apices of first and second basal cells clear 20
Apical spot noticeably widened beyond origin; occasionally separated from crossband, usually invading about ½ of cell R_4; femora variable in color; first and second basal cells may or may not be infuscated 21
20. Apical spot at its origin somewhat wider than cell R_1 ..... *sackeni* Hine*
Apical spot at its origin not wider than cell R_1 ..... *callidus* Osten Sacken
21. Body without yellow markings; usually definite cloud on base of vein R_4 at fork 22
Body with various yellow patterns; no cloud on fork 23
22. Outer margin of crossband noticeably bowed (see also couplet 33) ..... some *fuliginosus* Wiedemann*
Outer margin of crossband nearly straight ..... *brimleyi* Hine
23. Lateral facial calli and lower genae dark brown to black; abdomen fuscous with conspicuous middorsal yellow stripe attenuated caudally ..... *univittatus* Macquart
Face and cheeks entirely yellow 24
24. Second basal cell predominantly hyaline; abdomen pale yellow, often with indefinite light brown or fuscous markings, that on tergite two and inverted "V" usually not reaching anterior margin 25
Second basal cell at least ½ infuscated; abdominal pattern otherwise 29
25. Ground color of thoracic dorsum and scutellum typically yellow-brown 26
Ground color of thoracic dorsum and scutellum typically green-gray 27
26. Tergite two with broad pale translucent yellow basal band above flat, broad, brown inverted "V"; outer margin of crossband often gently sinuous; posterior hyaline areas along wing margin often lightly tinted ..... *reicherti* Fairchild
Base of tergite two straw yellow, about same color as others, median figure usually taller; outer margin of crossband straight; hyaline areas usually clear ..... *flavidus* Wiedemann
27. Inner margin of crossband dilute, bases of discal (first M_2) and R_3 cells extensively subhyaline ..... *cursim* Whitney
Inner margin of crossband practically filling discal and R_3 cells to their bases 28

Key to Males of Chrysops (continued)

28. First basal cell infuscated with prominent distal hyaline area; facial calli not noticeably swollen ..... *celatus* Pechuman
First basal cell entirely infuscated at least faintly; facial calli slightly protuberant ..... *pudicus* Osten Sacken
29. Abdomen quadrivittate, tergite two with sublateral black spots ..... *montanus* Osten Sacken
Abdomen not vittate, tergite two yellow on either side of median figure ..... *dimmocki* Hine
30. Body predominantly dark, abdomen sometimes with one or three light stripes 31
At least abdomen with extensive yellow and dark pattern 36
31. Femora and fore coxae black; usually no suggestions of abdominal stripes and no yellow thoracic stripes though pleura may have plumbeous markings 32
Femora and much of fore coxae yellow; sides of thorax and often abdomen with yellow stripes 34
32. Hyaline triangle sharply limited to apices of cells M_1 and M_2 (cell R_5 entirely infuscated) ..... *moechus* Osten Sacken
Hyaline triangle at least invading cell R_5 33
33. Outer border of crossband gently bowed, apex of hyaline triangle crossing vein R_{2+3}; small isolated spot at fork; hyaline areas in apices of basal cells ..... *brimleyi* Hine
Outer border of crossband sinuous, sometimes connecting along vein R_{4+5} with spot at fork, thus isolating diagonal dash in cell R_3, which represents apex of hyaline triangle; whole apex of wing and apices of basal cells may otherwise be tinted ..... *fuliginosus* Wiedemann*
34. No yellow stripe on thorax above wing base, gray to yellowish stripes confined to pleura ..... *parvulus* Daecke
Yellow stripe on each side of thorax above wing base 35
35. Abdomen with one or three definite yellowish lines ..... *obsoletus obsoletus* Wiedemann
Abdomen dark, at most trace of median line on tergite two ..... *obsoletus lugans* Wiedemann
36. Wing mostly infuscated except hyaline areas in distal portion of first basal cell, most of second basal cell, and along distal margin of crossband; abdominal pattern indefinite brown bands on pale yellow 37
Wing with hyaline areas usually more extensive, hyaline triangle usually open to hind margin; abdomen variable, usually striate 38
37. Dorsum of thorax grayish green with three fuscous stripes ..... *celatus* Pechuman
Dorsum of thorax with brown and yellow stripes ..... *reicherti* Fairchild
38. Apex of hyaline triangle nearly or quite reaching vein R_{2+3} and occasionally crossing it 39
Apex of hyaline triangle just enveloping fork 45
39. Apex of hyaline triangle usually terminating in cell R_3; abdomen with two to four black lines 40
Apex of hyaline triangle usually separating the apical spot from crossband; abdominal tergite two mostly yellow with or without pair of small dark dashes 41
40. Facial calli and lower gena predominantly brown to black 42
Facial calli and gena predominantly yellow, sometimes with narrow darkened area near lateral margin 43
41. Second abdominal segment with two submedian dashes ..... *geminatus geminatus* Wiedemann
Second abdominal segment yellow ..... *geminatus impunctus* Krober
42. Lateral abdominal stripes incomplete, not reaching tergite one ..... *pikei* Whitney
Lateral abdominal stripes complete to tergite one ..... *sequax* Williston
43. A median black figure on tergite two broadly joined to black figure of tergite one; the median yellow triangles do not reach anterior

Key to Males of Tabanus (continued)

borders of tergites ..... *montanus* Osten Sacken

Abdomen dorsally with four longitudinal dark stripes 44

44. Abdomen with four black lines equal in length and attaining tergite one; hind tibiae not swollen; cell Cu_1 and 2nd basal cell predominantly hyaline ..... *beameri* Brennan

Abdomen with two submedian black lines and two shorter sublateral lines which do not attain tergite one; hind tibiae slightly expanded; cell Cu_1 and 2nd basal cell considerably infuscated ..... *hinei* Daecke*

45. Abdominal pattern transverse; first basal cell hyaline in apex ..... occasional dark *flavidus* Wiedemann

Abdominal pattern linear; first basal cell infuscated to apex 46

46. Ground color of thorax and scutellum yellow ..... *vittatus* Wiedemann

Ground color of thorax and scutellum plumbeous 47

47. Dorsum of abdomen predominantly dark with trace of yellow on the sides and conspicuous yellow median stripe ..... *macquarti* Philip

Dorsum of abdomen predominantly yellow with four more or less complete black stripes, occasionally lateral ones reduced to small isolated spots ..... *striatus* Osten Sacken

Key to Females of Tabanus

1. Eye sparsely pilose; body length 10–14 mm; abdomen brownish with row of thin median spots and rounded sublateral spots; second palpal segment slender; wing hyaline; eye in life green with single diagonal purple band 2

Not agreeing entirely with the above 3

2. Frons 2.5–3.5 times as high as wide, the basal callus usually transverse; base of third antennal segment slender ..... *quaesitus* Stone

Frons about four times as high as wide, the basal callus higher than wide; base of third antennal segment rather stout ..... *exilipalpis* Stone*

3. Abdomen dorsally with both median and sublateral pale spots or triangles which may or may not be contiguous on consecutive tergites (sublateral spots very faint on *acutus* but midstripe prominent, coastal species) 4

Abdomen dorsally unicolorous (except dark markings on some *abdominalis*), or with single median row of pale spots or triangles which sometimes arise from pale apical bands; these bands may widen laterally but do not form distinct sublateral spots or triangles (sublateral pale spots sometimes present on tergite two only) 29

4. Abdomen dorsally with median, parallel-sided pale stripe 21

Abdomen dorsally with median row of pale spots or triangles, which may be contiguous but do not form parallel-sided stripe 5

5. Mesonotum covered with golden yellow hair, without longitudinal stripes; conspicuous middorsal golden abdominal stripe widening posteriorly on each tergite; frons ratio 1:5 or greater, widened above 6

Without this combination of characters 7

6. Palpi creamy yellow; genae and pleurae with yellow hair; third antennal segment with annulate part black; femora gray to black ..... *fulvulus* Wiedemann

Palpi white; genae and pleurae with white hair; third antennal segment usually orange, often annulate portion darkened; femora yellowish ..... *pallidescens* Philip

7. Length usually 12 mm or more; frons variable, usually parallel-sided or only slightly widened above 8

Length less than 12 mm; frons distinctly widened above; dark gray to black species 19

8. Wing distinctly mottled or varie-

Key to Females of Tabanus (continued)

gated; frons ratio approximately 1:3 ..... *venustus* Osten Sacken

Wing not variegated; frons ratio variable 9

9. Dark gray species with hyaline wing; third antennal segment with basal portion entirely black; second palpal segment stout; eye in life with single band ..... *fairchildi* Stone

Without this combination of characters 10

10. Wing mostly hyaline with conspicuous isolated spots on cross veins and fork; moderate to large, dark gray species 11

Wing without conspicuous isolated spots on cross veins and fork; medium to small, dark brown to orange-brown species 12

11. Frons ratio approximately 1:4.5; basal callus distinctly higher than wide ..... *cymatophorus* Osten Sacken

Frons ratio 1:2.5–1:3; basal callus subquadrate ..... *reinwardti* Wiedemann

12. All wing veins margined with brown; frons ratio 1:3 to 1:3.5 ..... *gracilis* Wiedemann*

Longitudinal veins not margined with brown 13

13. Third antennal segment uniformly orange-brown; eye in life with two bands; dorsum of thorax with yellowish cast ..... *zythicolor* Philip

Third antennal segment with annulate part black; number of eye bands variable; thorax usually darker 14

14. Frons ratio less than 1:3; eye in life with single band (coastal species) ..... *texanus* Hine

Frons ratio 1:3 or greater; eye in life with two or more bands 15

15. Frons ratio 1:4 to 1:5; plate of third antennal segment only slightly longer than broad; costal cell rather intensely yellow; legs primarily yellowish brown; fore femora, apices of tibiae, and tarsi, darkened ..... *longiusculus* Hine

Without this combination of characters 16

16. Frons broad, ratio approximately 1:3; 2nd palpal segment swollen at base ..... *sagax* Osten Sacken

Frons narrow, ratio usually greater than 1:3.5; 2nd palpal segment usually not much enlarged 17

17. Frons distinctly widened above ..... *sackeni* Fairchild*

Frons at most only slightly widened above 18

18. Frons ratio less than 1:5; plate of third antennal segment long and slender, about twice as long as width at widest portion ..... *sublongus* Stone

Frons ratio greater than 1:5; plate of third antennal segment broad, only slightly longer than width at widest portion ..... *wilsoni* Pechuman

19. Eye in life or relaxed specimens with two bands; median callus subquadrate; palpus not strongly swollen basally and not sharply pointed ..... *pumilus* Macquart

Eye unicolorous or with one purple band; median callus slender; palpus strongly swollen basally with apex acute 20

20. Eye unicolorous ..... *sparus* Whitney*

Eye with single purple band ..... *sparus milleri* Whitney

21. Length 16–21 mm; fork with small dark spot ..... *acutus* (Bigot)

Length usually 9–15 mm; fork without dark spot 22

22. Eye in fresh or relaxed specimens with single reddish purple band; frons nearly parallel-sided; costal cell colored, sometimes faintly 23

Eye in fresh or relaxed specimens with at least 2 bands; frons usually widened above; costal cell as hyaline as rest of wing 27

23. Palpi and pleurae yellow to creamy yellow; costal cell infuscated; dorsum of thorax yellowish usually with conspicuous golden pollinosity 24

Palpi white or creamy white; pleurae grayish, dorsum usually grayish to cinereous, occasionally yellowish; costal cell variable 25

24. Frons ratio 1:3.4 or less (coastal

Key to Females of Tabanus (continued)

species of Louisiana and Texas) ... *eadsi* Philip

Frons ratio usually about 1:3.5 or greater ... *quinquevittatus* Wiedemann*

25. Abdomen predominantly yellowish laterally; costal cell yellowish to clear; femora mostly black (coastal species) ... *nigrovittatus* Macquart

Abdomen tan to dark brown or black laterally, sublateral pale spots faint; costal cell deeply infuscated; femora variable ... 26

26. Basal callus usually brown; legs usually yellowish brown to dark brown; abdomen light to medium brown with light median stripe and small sublateral rounded spots ... *fuscicostatus* Hine

Basal callus dark brown to black; femora, apical portions of tibiae and tarsi, black; abdomen dorsally dark brown to black at least posteriorly, with light median stripe and occasionally faint sublateral spots ... *mularis* Stone

27. Scutellum reddish at posterior margin ... *subsimilis* Bellardi

Scutellum and thorax concolorous, dark ... 28

28. Abdomen predominantly yellow-brown; the two submedian dark stripes reduced (coastal form) ... *lineola hinellus* Philip

Dorsum of abdomen predominantly dark with sublateral pale stripes reduced ... *lineola lineola* Fabricius

29. Abdomen unicolorous, usually dark, lacking middorsal triangles (some *abdominalis* with median dark spots) ... 30

Abdomen bicolorous; faint to distinct pale median triangles or spots with or without apical bands, or bands only ... 41

30. Abdomen deep reddish brown to reddish purple; wing hyaline with furcation and cross veins distinctly margined with brown, costal cell brown; prominent tufts of hair above and below wing base; frons 3–3.5 times higher than basal width, parallel sided; antennae orange ... 64

Without above combination of characters ... 31

31. Subcallus protuberant, shiny; wing dark brown, no distinct spot at furcation ... 32

Subcallus pollinose, not protuberant; wing variable ... 33

32. At least upper ½ of genae shiny brown to black; frons ratio approximately 1:2 to 1:2.5 ... *atratus* Fabricius

Genae pollinose; frons ratio 1:3 to 1:4 ... *wiedemanni* Osten Sacken

33. Reddish brown species; antennae brown; frons widened above, ratio 1:6.5 or greater; occasionally very faint small abdominal triangles; wings faintly tinted, occasionally with faint spots at furcation and cross veins, cell R_5 not narrowed apically ... *aar* Philip

Without above combination of characters ... 34

34. Hair of genae and pleurae, pale to yellow ... 35

Genae (at least hair), and entire pleurae dark brown to black ... 37

35. Spot at furcation; fore femora black ... 68

No spot at furcation; fore femora orange to reddish brown ... 36

36. Wing hyaline, costal cell dark brown; genae orange yellow; pronounced tufts of white hair above and below wing base ... *americanus* Forster

Wing uniformly dilute brown; genae pale to gray; tufts at wing base not especially pronounced ... *calens* Linnaeus

37. Frons ratio approximately 1:6, widened above; median callus long and slender; wings subhyaline with prominent spot at furcation; thorax deep reddish brown to reddish purple ... *proximus* Walker

Frons ratio less than 1:5.5 and differing in at least one other character ... 38

38. Abdomen black with bluish pruinosity; 3rd antennal segment mostly black; frons ratio approximately

Key to Females of Tabanus (continued)

1:4 to 1:5; wing uniformly dark ..... *aranti* Hays
Not agreeing entirely with above 39
39. Mesonotum covered with distinct white hair and pollen ..... *stygius* Say
Mesonotum dark brown to black 40
40. Wing nearly hyaline distad of basal cross vein ..... *nigrescens* Palisot de Beauvois*
Wing nearly uniformly dark ..... *colon* Thunberg
41. Fork without infuscation 42
Fork with infuscation, either distinct spot or extension of vein margin infuscation (spot faint in some *coarctatus, equalis, molestus,* and *turbidus*) 51
42. Medium sized fly; scutellum with distinct white pile; abdomen with conspicuous pale triangles or spots, spot on tergite 2 distinctly smaller than those on tergites 3 and 4; abdominal venter without median dark stripe 55
Without above combination of characters 43
43. Medium sized brownish fly with median row of pale abdominal triangles; wing clear, costal cell deeply infuscated; frons approximately 4.5 times higher than basal width; third antennal segment dirty orange; legs entirely brownish ..... *kisliuki* Stone*
Without above combination of characters 44
44. Median abdominal spots, if present, not contrasting sharply with remainder of tergites; palpi slender, tan to reddish brown 45
Contrasting median abdominal triangles present dorsally; palpi thicker basally, whitish to cream colored 47
45. Medium sized fly; costal cell hyaline to faintly tinted ..... *rufofrater* Walker
Large fly; costal cell yellow or brown 46
46. Wing hyaline, costal cell dark brown; abdomen usually with apical bands ..... *americanus* Forster
Wing uniformly dilute brown ..... *calens* Linnaeus
47. Subcallus denuded or very thinly pollinose; small compact fly not over 16 mm long; brownish black with single median row of triangles on abdomen arising from pale posterior bands; fore tibiae not distinctly bicolored, although there may be pale hair basally ..... *nigripes* Wiedemann
Subcallus not denuded 48
48. Abdomen black with median white triangles confined to segments 3–5; if very small triangle remains on tergite two, then fore tibiae entirely dark 49
Abdomen gray to brownish black, white median triangles or spots on segments 1–6 50
49. Fore tibiae distinctly bicolored; no median spot on abdominal tergite two although two sublateral pale spots may sometimes be present ..... *trimaculatus* Palisot de Beauvois
Fore tibiae entirely dark; very small median pale spot on abdominal tergite two ..... *superjumentarius* Whitney*
50. Cell R_5 narrowed to closed; abdominal triangle of tergite two sometimes not attaining anterior margin; hind tibia usually with extreme apex dark ..... *melanocerus* Wiedemann
Cell R_5 usually petiolate; abdominal triangle of tergite two usually attaining anterior margin, slightly expanded; hind tibiae usually entirely yellowish ..... *petiolatus* Hine
51. Abdomen with contrasting, pale median spots or triangles 52
Abdomen with indistinct median spots or triangles 63
52. No median spot on tergite two; fore tibia distinctly bicolored; venter of abdomen with distinct median brownish black stripe ..... *trimaculatus* Palisot de Beauvois
Median pale spot usually present on tergite 2 or at least posterior margin pale; differing in at least one other character 53

Key to Females of Tabanus (continued)

53. Median spot on tergite 2, if present, distinctly smaller than those on tergites three and four; scutellum with distinct pale pile 54
Without this combination of characters 56

54. Abdomen black with small median triangles; venter grayish with wide median black stripe ..... *superjumentarius* Whitney*
Abdominal triangles rather large and broad; venter not as above 55

55. Frons less than six times as high as basal width, only moderately widened above; middle and hind tibiae pale to dark reddish brown, apices not markedly darker ..... *molestus* Say
Frons more than 6 times as high as basal width, wider above; middle and hind tibiae creamy white, extreme apices dark ..... *moderator* Stone

56. Fore tibia bicolored, basal part yellowish brown to cream with pale hair, apical part dark brown with black hair ..... *sulcifrons* Macquart
Fore tibia unicolorous, or rarely base brownish with orange hair and apex darker 57

57. Venter of abdomen black with strongly contrasting, rather broad white bands ..... *trijunctus* Walker*
Venter of abdomen brownish, pale bands, if present, not strongly contrasting 58

58. Medium sized; plate of third antennal segment with very slight or no dorsal excision; frons ratio approximately 1:4 with parallel sides; basal callus, antennae, palpi, legs, mostly brown; abdomen brown with gray median triangles; tergites with grayish posterior margins which expand laterally; wing almost hyaline with infuscation at fork and cross veins; cell R_5 somewhat narrowed apically; body length usually less than 18 mm ..... *endymion* Osten Sacken
Without this combination of characters 59

59. Frons ratio 1:5 or greater; legs uniformly orange brown; cell R_5 closed or strongly narrowed apically; wings subhyaline with dark infuscation at fork and cross veins; abdomen brown with median row of small grayish yellow triangles ..... *nefarius* Hine
Without this combination of characters 60

60. Abdomen dorsally orange brown or grayish brown with moderate to rather large median triangles 61
Abdomen dark reddish purple to nearly black with small median white spots that may be longer than broad 64

61. Cell R_5 narrowed apically; frons ratio 1:4 to 1:5.6; fore femora dark brown to black ..... *sulcifrons* Macquart
Not agreeing entirely with above 62

62. Frons 2.5–3.5 times as high as wide with parallel sides; cell R_5 narrowed apically ..... *cheliopterus* Osten Sacken
Frons about four or more times as high as basal width, widened above; cell R_5 not narrowed apically 70

63. Deep reddish brown to reddish purple species; prominent tufts of hair around wing base; wing hyaline to subhyaline with dark infuscation at furcation and cross veins; antenna, palpus, legs, orange brown; subcallus, clypeus, genae, yellowish brown; frons ratio approximately 1:3 to 1:3.5 64
Without this combination of characters 65

64. Plate of 3rd antennal segment dorsally with prominent forward-projecting tooth-like process; eye in life or relaxed specimens with narrow median band and broad band at lower eye margin ..... *imitans* Walker
Dorsal process of plate without prominent tooth-like process; eye in life or relaxed specimens with 2 median bands ..... *maculipennis* Wiedemann

Key to Females of Tabanus (continued)

65. Cell R_5 narrowed or closed apically ... 66
Cell R_5 not narrowed apically ... 69
66. Frons ratio 1:5 or greater; legs uniformly orange-brown; cell R_5 closed or strongly narrowed apically; wings subhyaline with dark infuscation at fork and cross veins; abdomen brown, median row of triangles faint or absent ... *nefarius* Hine
Without this combination of characters ... 67
67. Legs predominantly orange-brown ... *cheliopterus* Rondani
Legs, at least femora, predominantly black ... 68
68. Abdomen reddish brown; mesonotum with lavender tone and narrow gray lines; hind tibia reddish brown to dark brown; palpus slender, strap-like, with apex truncate ... *gladiator* Stone
Abdomen orange; mesonotum yellowish with dark lines; hind tibia orange except apical ¼, which is dark brown to black; palpus moderate in width, tapering to narrow apex ... *abdominalis* Fabricius
69. Clypeus, genae, and pleurae brownish with concolorous hair; abdomen orange-brown with at most only faint suggestions of middorsal triangles, occasionally lateral margins dark; body length 18–25 mm ... *aar* Philip
Clypeus, genae, and pleurae gray to grayish brown with pale hair; abdomen with or without faint middorsal triangles, usually with lateral pale areas arising from pale posterior margins of each tergite ... 70
70. Costal cell clear; legs brown, fore femora dark brown to black; hair on fore femora black, tibial fringes mostly black; white or mixed black and white hair on rest of legs ... *rufofrater* Walker
Costal cell infuscated; legs uniformly reddish to reddish brown with white or concolorous hair ... 71
71. Third antennal segment entirely black, basal portion with rather obtuse dorsal process and only slight dorsal excision; palpi beige with mostly pale hair; wing veins not margined with brown (occasionally margin of R_{2+3} lightly tinted); body length usually less than 17 mm ... *coarctatus* Stone
Not agreeing entirely with above ... 72
72. Wing veins margined with brown; frons usually six or more times greater than basal width; third antennal segment mostly orange ... *turbidus* Wiedemann
Wing veins usually not margined or at most faintly margined with brown; frons height usually 5.5 times or less than basal width; third antennal segment mostly black ... *equalis* Hine

Key to Males of Tabanus (not including *exilipalpis, kisliuki,* and *nefarius*)

1. Eye with dense long pile; body length 10–14 mm; antenna slender; abdomen brownish with row of thin median spots and rounded sublateral spots ... *quaesitus* Stone
Not agreeing entirely with above ... 2
2. Abdomen dorsally with both median and sublateral pale spots or triangles, or sublateral spots only; median pale markings may form parallel-sided stripe (sublateral spots very faint but median stripe pronounced on *acutus*, coastal species) ... 3
Abdomen dorsally unicolorous (except dark markings on some *abdominalis* and *gladiator*), or with single median row of pale spots or triangles, which sometimes arise from pale apical bands; these bands may widen laterally but do not form distinct sublateral spots or triangles; (sublateral pale spots sometimes present on tergite two only) ... 27
3. Abdomen dorsally with median, parallel-sided pale stripe ... 19
Abdomen dorsally with median row of pale triangles or spots, which may be contiguous but do not form parallel-sided stripe; some-

Key to Males of Tabanus (continued)

times only sublateral spots present 4

4. Length 11 mm or less; small dark gray to brownish species; costal cell hyaline; median abdominal triangles faint or absent, sublateral spots rounded 5
   Length 11 mm or more; if less, costal cell infuscated 7
5. Femora mostly brownish, concolorous with tibiae or nearly so; eye in life or relaxed specimens with two narrow green bands, the upper partially covered by large facets ..... *pumilus* Macquart
   Femora mostly black, basal portion of tibiae light tan; eye in relaxed specimens with single purple band or none 6
6. Eye with single purple band ..... *sparus milleri* Whitney
   Eye without band ..... *sparus* Whitney*
7. Dark gray species; third antennal segment with plate entirely black; wing hyaline without spot at furcation ..... *fairchildi* Stone
   Without this combination of characters 8
8. Wing mostly hyaline with conspicuous isolated spots on cross veins and fork 9
   Wing without conspicuous isolated spots on cross veins and fork 10
9. Eye bare to sparsely pilose, upper and lower eye facets strongly differentiated; antennae mostly orange ..... *cymatophorus* Osten Sacken
   Eye distinctly pilose, upper and lower eye facets not sharply differentiated; antennae mostly blackish ..... *reinwardti* Wiedemann
10. Costal cell darkly infuscated 11
    Costal cell clear or faintly tinged yellow 13
11. Antenna entirely light orange ..... *zythicolor* Philip
    Antenna with annulate portion black 12
12. Sublateral abdominal spots extensive and contiguous (coastal species) ..... *texanus* Hine
    Sublateral abdominal spots reduced and isolated ..... *longiusculus* Hine
13. Palpi creamy yellow; genae and pleurae with yellow hairs; third antennal segment with annulate portion black; femora gray to black; areas of large and small eye facets not sharply differentiated ..... *fulvulus* Wiedemann
    Without this combination of characters 14
14. Hair of thoracic dorsum yellow; sublateral abdominal spots yellow 15
    Hair of thoracic dorsum gray to dark; sublateral abdominal spots pale brownish gray or brownish yellow 17
15. Annulate portion of third antennal segment usually yellowish; conspicuous golden yellow pollen and pile on dorsum of thorax; palpi white to creamy ..... *pallidescens* Philip
    Annulate portion of third antennal segment black; ground color of thoracic dorsum gray with golden yellow pile; palpi variable 16
16. Median abdominal stripe broad; hair of genae yellowish white; second palpal segment stout, yellow-brown ..... *sagax* Osten Sacken
    Median abdominal stripe narrow; hair of genae pale gray; second palpal segment relatively slender, creamy white ..... *sublongus* Stone
17. Third antennal segment uniformly orange-brown; wing veins usually margined with brown ..... *gracilis* Wiedemann*
    Third antennal segment with annulate portion black; wing veins not margined with brown 18
18. Areas of large and small eye facets sharply differentiated ..... *sackeni* Fairchild*
    Areas of large and small eye facets not sharply differentiated ..... *wilsoni* Pechuman
19. Fork with small dark spot ..... *acutus* (Bigot)
    Fork without dark spot 20
20. Annulate portion of third antennal segment as long or longer than base; costal cell usually infuscated 21

Key to Males of Tabanus (continued)

Annulate portion of third antennal segment shorter than base; costal cell hyaline ... 25

21. Palpus, pleura, costal cell yellowish; thorax and yellowish stripe of abdomen golden pollinose ... 22
Palpus white or creamy white; pleura grayish; dorsum usually grayish to cinereous; costal cell variable ... 23

22. Costal cell brownish; gena, pleural pile, light yellow; (coastal species of La. and Texas) ... *eadsi* Philip
Costal cell yellow; gena, pleural pile, darker yellow ... *quinquevittatus* Wiedemann*

23. Eye in life or relaxed specimens with single reddish purple band readily visible just beneath upper eye facets; abdomen predominantly yellowish laterally; costal cell yellowish to clear (coastal species) ... *nigrovittatus* Macquart
Without this combination of characters ... 24

24. Legs predominantly yellowish brown; abdomen extensively yellowish brown ... *fuscicostatus* Hine
Femora, apical portions of tibiae and tarsi, black; abdomen predominantly dark brown to black, at least so apically ... *mularis* Stone

25. Scutellum reddish at posterior margin ... *subsimilis* Bellardi
Scutellum and thorax concolorous, dark ... 26

26. Palpi usually pale yellow; median pale abdominal stripe broad (coastal form) ... *lineola hinellus* Philip
Palpi creamy white; median pale abdominal stripe thinner ... *lineola lineola* Fabricius

27. Abdomen unicolorous, except dark abdominal markings on some *abdominalis* and *gladiator* ... 28
Abdomen bicolorous; faint to distinct pale median triangles or spots with or without apical bands, or bands only ... 39

28. Fork without dark spot, although whole wing may be infuscated ... 29
Fork with distinct dark spot ... 32

29. Entirely black species ... 30
Otherwise colored ... 42

30. Frontal triangle and genae shiny brown to black ... *atratus* Fabricius
At least genae pollinose ... 31

31. Frontal triangle pollinose and flattened in profile ... *aranti* Hays
Frontal triangle denuded and somewhat raised in profile ... *wiedemanni* Osten Sacken

32. Deep reddish brown to reddish purple species; tufts of prominent hair around wing base; wing hyaline to subhyaline with dark infuscation at furcation and cross veins; antennae, palpi, legs, orange-brown; clypeus, genae, yellowish to grayish yellow; upper eye facets distinctly enlarged, sharply differentiated from lower facets ... 58
Without this combination of characters ... 33

33. Genae light to dark gray ... *proximus* Walker
Genae dark brown or yellow; if genae gray then abdomen reddish orange ... 34

34. Abdomen black, first tergite with bluish pruinosity; third antennal segment entirely black ... *aranti* Hays
First abdominal tergite lacking bluish pruinosity; antennae variable, not entirely dark ... 35

35. Wing almost uniformly dark ... *colon* Thunberg
Wing subhyaline or at least lighter apically ... 36

36. Antenna mostly orange; entirely dark chocolate brown species, dorsum of thorax with lighter hair and ground color ... *stygius* Say
Not agreeing entirely with above; if entirely dark species, thorax concolorous with rest of body, antenna usually with at least annulate part brown ... 37

37. Abdomen blackish brown; entirely chocolate brown species ... *nigrescens* Palisot de Beauvois*
Abdomen orange to reddish brown ... 38

Key to Males of Tabanus (continued)

38. Cell R_5 not narrowed apically ..... *aar* Philip
Cell R_5 narrowed or closed apically .. 61
39. Wing variegated; first tergite black, second with narrow, sometimes incomplete, posterior, pale band nearly uniform in width ..... *venustus* Osten Sacken
Not as above 40
40. Fork without infuscation 41
Fork with infuscation, either distinct spot or extension of vein margin infuscation (faint in some *aar, equalis, turbidus* and *coarctatus,* and legs reddish to orange-brown) 48
41. Median abdominal spots, if present, not contrasting sharply with remainder of tergites 42
Median abdominal triangles present dorsally and contrasting with dark brown to black abdomen; if faint, frontal triangle shiny, denuded 44
42. Medium sized fly; costal cell hyaline ..... *rufofrater* Walker
Large fly; costal cell yellow or brown 43
43. Wing hyaline, costal cell dark brown; abdomen usually with apical bands ..... *americanus* Forster
Wing uniformly dilute brown ..... *calens* Linnaeus
44. Scutellum with distinct white pollen and pile, thorax darker with brown stripes 51
Scutellum without white pollen and pile except around margin; or, if present, not contrasting sharply with that of thorax 45
45. Frontal triangle denuded, shiny, swollen; brownish black species with single median row of triangles on abdomen arising from pale posterior bands ..... *nigripes* Wiedemann
Without this combination of characters 46
46. Abdominal triangles wanting at least on tergite 2 ..... *superjumentarius* Whitney*
Abdominal triangle present on tergite 2 47
47. Enlarged eye facets occupying about ½ the total area of eye; cell R_5 usually petiolate ..... *petiolatus* Hine
Enlarged eye facets occupying ⅔ to ¾ total area of eye; cell R_5 usually narrowed but not petiolate ..... *melanocerus* Wiedemann
48. Abdomen with contrasting, pale median spots or triangles 49
Abdomen with indistinct median spots or triangles 57
49. No median spot on tergite two; fore tibia usually bicolored; areas of large and small eye facets distinctly differentiated; dorsum of abdomen blackish with three median white triangles; venter of abdomen with distinct median black stripe; furcation and cross veins faintly margined with brown ..... *trimaculatus* Palisot de Beauvois
Without this combination of characters 50
50. Median spot on tergite two, if present, distinctly smaller than those on tergites three and four; scutellum with distinct pale pile; fore tibia nearly uniform in color (some *moderator* with extreme base pale) 51
Without this combination of characters 52
51. Middle and hind tibiae pale to dark reddish brown, apices not markedly darker ..... *molestus* Say
Middle, hind tibiae creamy white, extreme apices dark brown to black ..... *moderator* Stone
52. Plate of third antennal segment mostly orange with prominent dorsal excision, annulate portion black; palpi and fore femora dark brown to black; upper eye facets distinctly enlarged, sharply differentiated from lower; abdomen orange-brown ..... *sulcifrons* Macquart
Without this combination of characters 53
53. Venter of abdomen black with strongly contrasting, rather broad white bands ..... *trijunctus* Walker*
Venter of abdomen brownish; pale bands, if present, not strongly contrasting 54

Key to Males of Tabanus (continued)

54. Medium sized; plate of third antennal segment with very slight or no dorsal excision; antennae, palpi, legs, mostly brown; abdomen brown with gray median triangles which may be somewhat flattened and obscured by apical bands; tergites with grayish posterior margins which expand laterally; wing almost hyaline with infuscation at fork and cross veins; cell R_5 somewhat narrowed apically ..... *endymion* Osten Sacken

Without this combination of characters 55

55. Abdomen dorsally orange-brown or grayish brown with rather large median triangles 56

Abdomen dark reddish purple to nearly black with small median white spots that may be longer than broad 58

56. Antennae wholly orange; enlarged facets occupying ¾ total area of eye; cell R_5 narrowed apically ..... *cheliopterus* Osten Sacken

Not as above 64

57. Deep reddish brown to reddish purple species; tufts of prominent hair around wing base; wing hyaline to subhyaline with dark infuscation at furcation and cross veins; antenna, palpus, legs, orange-brown; clypeus, genae, yellowish to grayish yellow; upper eye facets distinctly enlarged, sharply differentiated from lower facets 58

Without this combination of characters 59

58. Plate of 3rd antennal segment dorsally with prominent forward-projecting tooth-like process ..... *imitans* Walker

Dorsal process of plate without prominent tooth-like process ..... *maculipennis* Wiedemann

59. Cell R_5 narrowed or closed apically 60

Cell R_5 not narrowed apically 62

60. Legs predominantly orange-brown ..... *cheliopterus* Rondani

Legs, at least femora, predominantly black 61

61. Mesonotum with lavender tone, with narrow gray lines; eye facets not noticeably differentiated ..... *gladiator* Stone

Mesonotum yellowish with dark lines; upper eye facets moderately enlarged, differentiated from lower facets ..... *abdominalis* Fabricius

62. Legs, especially fore femora, dark brown to black; hair on fore femora black, tibial fringes mostly black; black or mixed black and white hair on rest of legs; pale abdomen contrasting with dark brown thorax; posterior pale bands of tergites wide, nearly obscuring median pale triangles ..... *rufofrater* Walker

Without above combination of characters; legs uniformly reddish to reddish brown with white or concolorous hair 63

63. Clypeus, genae, and pleurae, brown with concolorous hair; abdomen orange-brown with at most only faint suggestions of middorsal triangles, occasionally lateral margins dark ..... *aar* Philip

Clypeus, genae, and pleurae, gray to grayish brown with pale hair; abdomen with or without faint middorsal triangles, usually with lateral pale areas arising from the pale posterior margins of each tergite 64

64. Third antennal segment black except at extreme base; annulate portion shorter than basal portion, latter with only slight dorsal excision; costal cell distinctly infuscated; upper eye facets moderately enlarged, areas of large and small facets not sharply differentiated ..... *coarctatus* Stone

Not agreeing entirely with above 65

65. Wing veins distinctly margined with brown; third antennal segment mostly orange; upper eye facets distinctly enlarged, differentiated from lower facets ..... *turbidus* Wiedemann

Wing veins usually not margined

with brown at most only faint trace of infuscation; third antennal segment mostly dark; upper eye facets only moderately enlarged, line of demarcation between large and small facets not distinct ..... *equalis* Hine

Key to Species of Hybomitra

1. Clypeus and gena shiny black; much of wing infuscated ..... *hinei* (Johnson)*
   Not as above 2
2. Black species with broad band of orange across first three abdominal segments; wings dark ..... *cincta* (Fabricius)
   Coloration not as above 3
3. Subcallus pollinose; wings entirely infuscated ..... *trispila* (Wiedemann)
   Subcallus bare; wings with at least distal or apical regions clear 4
4. Wings with prominent infuscation at furcation and cross veins; abdomen broadly yellowish orange laterally ..... *lasiophthalma* (Macquart)
   Wing mostly hyaline with costal cell and wing base infuscated; abdomen not as above ..... *difficilis* (Wiedemann)

Key to Species of Agkistrocerus

1. Hind margins of tergites and sternites with black hair; longitudinal veins in basal ⅔ of wing broadly margined with brown; median callus of female broadly joined to basal callus ..... *megerlei* (Wiedemann)
   Hair on lateral margins of tergites and hind margins of sternites pale; longitudinal veins basally not broadly margined with brown; median callus very slender line ..... *finitimus* (Stone)*

Key to Species of Hamatabanus

1. Abdomen with 3 rows of pale spots; wing hyaline ..... *carolinensis* (Macquart)
   Abdomen without sublateral pale spots; wing with at least costal cell brown 2
2. Dorsum of abdomen with dark median portion; antennae nearly black ..... *annularis* (Hine)
   Dorsum of abdomen without noticeably darkened median portion; antennae mostly orange ..... *sexfasciatus* (Stone)*

Species Accounts

In the following section, a general descriptive statement is included for all species recorded from Louisiana and several from neighboring states that are likely to occur in Louisiana. Morphological variations and ecological and distributional information are given for most species. Specimens were checked for variations by comparing them to the original descriptions and/or the descriptions given by Brennan (1935) and Stone (1938). The brief descriptions and variations are based primarily on Louisiana females unless otherwise indicated. It should be remembered that eye patterns are usually absent in dried material, and the patterns referred to herein are based on either live or relaxed specimens. The number of specimens examined refers to only those studied for variations and may not indicate the actual numbers collected. The seasonal distribution of common Louisiana Tabanidae is presented in Table II.

Changes in taxonomic status are presented for 4 species and subspecies including the synonymies of *Chrysops fulvistigma dorsopunctus* Fairchild and *Tabanus molestus mixis* Philip. *Chrysops flavidus reicherti* Fairchild and *T. maculipennis imitans* Walker are returned to specific rank. *Chrysops* ***harmani***, new species, is described; and larval descriptions based on specimens reared by the author are given for 33 species.

Subfamily Chrysopinae

Genus Merycomyia Hine, 1912

Only two Nearctic species are placed in this genus. They are robust *Tabanus*-like with small hind tibial spurs, well-developed ocelli, and the third antennal segment with three divisions (two annuli).

Merycomyia whitneyi (Johnson, 1904)

Length approximately 20 mm; abdomen dark to reddish brown, tergites four and five with distinct white patches; wing hyaline

TABLE II. Seasonal distribution of common Louisiana Tabanidae.

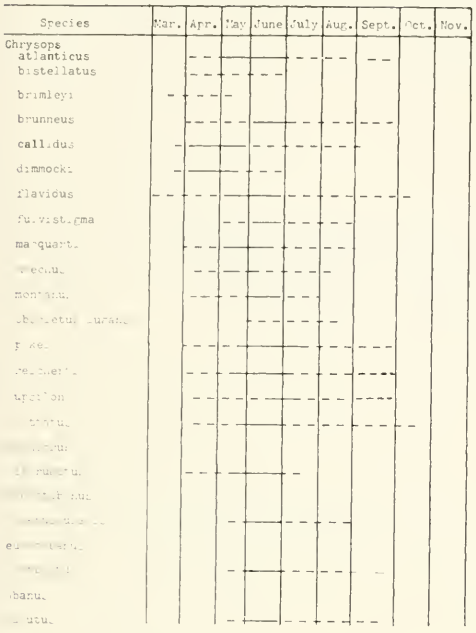
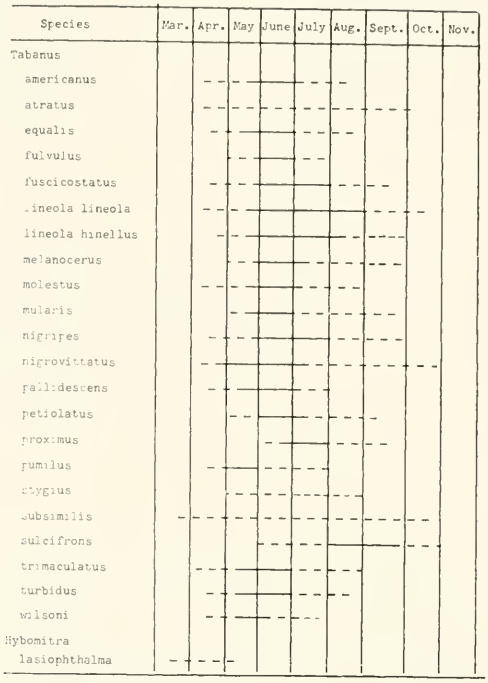


TABLE II. (*Continued*)



with veins faintly to strongly margined with brown.

Mature larva (Fig. 23): Approximately 40 mm long; creamy yellow with light brownish pubescent markings.

Head capsule length: Approximately 5.5 mm.

Striations: Irregular and widely-spaced laterally on segments 3–10 and at the posterior lateral margins of segments one and two; incomplete and broken dorsally and especially scanty on the ventral aspects of abdominal segments 1–7. Irregular striations present laterally on the anal segment, wide and conspicuous ventrally behind the anus; absent on the dorsum.

Thorax: Pubescence consisting of narrow pro-, meso-, and metathoracic annuli; lateral projections absent.

Abdominal segments 1–7: Anterior pubescence encircling segment one, progressively reduced laterally on segments 2–7 and ventrolaterally on segments 5–7. Pseudopodial pubescence encircles segments one and two, joined with anterior pubescence dorsolaterally on segment one and ventrolaterally on at least segments 1–3. Posterior pubescence present on segments 5–7 varying from a midventral patch on segment five to a band encircling segment seven.

Anal segment: Pubescence consisting of anal and posterior rings, the latter broadly encircling the segment.

Respiratory siphon: Consisting of two conspicuous lateral sclerotized plates, pointed apically and joined dorsally and ventrally by striated integument. A rigid prominent spine extends from between and well beyond the two plates.

Comments: This species was not collected in Louisiana; however, three larvae (one reared) were collected in the marginal region of a small lake in northwest Florida. The larvae were taken from sandy clay mud about ½ meter beneath the water's surface. This lake was located in a longleaf-slash pine forest region.

Genus SILVIUS Meigen, 1820

Most Nearctic species of this genus are Western in distribution. Only one species,

S. quadrivittatus (Say), is reported east of the Mississippi River. Members of the genus have denuded eyes speckled with small irregular spots, ocelli present, pedicel of antenna about ½ or less the length of the scape, and third antennal segment with five divisions (four annuli).

Silvius quadrivittatus (Say, 1823)

Length 6–10 mm; gray and brown; abdomen grayish with 4 rows of brown spots; wing hyaline, spotted with brown.

Variations: (Specimens examined—29) All agree with Brennan's (1935) description.

Ecology and Distribution: (May–August) An isolated population of this species was found in West Feliciana Parish in the upland hardwood region.

Genus CHRYSOPS Meigen, 1803

Commonly known as deer flies, members of this genus are relatively small and rarely exceed 12 mm. They are characterized by the presence of ocelli; denuded, brightly patterned eyes; a prominent frontoclypeus; third antennal segment with five divisions (four annuli), the basal one elongated; pedicel of antenna more than ½ as long as scape; hind tibiae with two apical spurs; and wings usually with an infuscated pattern.

Chrysops abatus Philip, 1941
(Fig. 41)

Length 7–9 mm; abdomen yellowish, darker posteriorly, with a median middorsal black stripe; face with median pollinose stripe; apex of hyaline triangle extending beyond wing vein R_{2+3}.

Variations: (Specimens examined—98) Departures from Philip's (1941) description include the following: midfacial stripe complete to oral margin in only 12 specimens, usually extending approximately ¾ the distance to oral margin; four specimens with posterior margin of wing infuscated; most specimens with legs black, basal portion of fore tibiae and basal ¾ or less of middle tibiae, dirty yellow; 1st tarsal segment on middle and hind legs mostly yellow to brownish yellow.

Ecology and Distribution: (April–May) Five specimens of this early season species were collected from the Gulf coastal longleaf-slash pine forests in Mississippi, and 93 were taken from similar forest types in St. Tammany and Tangipahoa parishes, Louisiana.

Chrysops amazon hubbelli Philip, 1955
(Fig. 42)

Length 9–12 mm; black; face with median pollinose stripe; pleura of female with dense orange pile; apical wing spot distinct reaching into ½ of cell R_4, anal and basal areas infuscated with hyaline spots in distal portion of basal cells.

Variations: (Specimens examined—16) In general the specimens agree with Philip's (1955) comparative description.

Ecology and Distribution: (April–May) This melanistic subspecies of *C. amazon* was collected from longleaf-slash pine forests in Tangipahoa and Washington parishes.

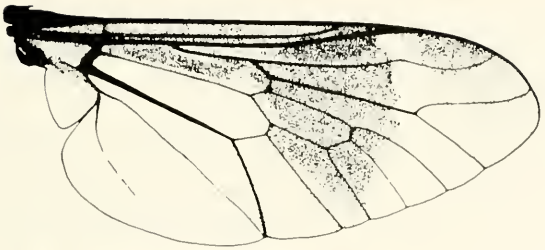
Chrysops atlanticus Pechuman, 1949
(Fig. 43)

Length 7–11 mm; mesonotum typically grayish green with dark stripes; abdomen yellowish with brown pattern; usual hyaline areas of wing dilutely infuscated.

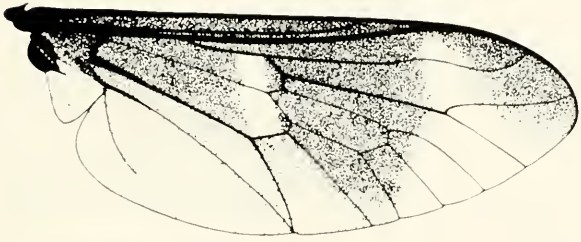
Variations: (Specimens examined—60) This species and *C. brunneus* represent coastal marsh forms of the *C. flavidus* complex in Louisiana. This complex is a confusing one as is illustrated by a statement from Pechuman (1949):

> The species which the writer has called *C. atlantica* has been known for some time but has been confused with *flavida* Wied. and *brunnea* Hine. Krober (1926, p. 291) apparently had both *atlantica* and *flavida* before him when he redescribed *flavida*. Philip (1941, p. 118) refers under *flavida* to "a northern form which approaches *brunnea* Hine." Daecke (1907, p. 146) mentions specimens of *flavida*, "in a measure resembling *brunneus*" and his figure 33A on plate VI is an excellent delineation of the wing of *atlantica*. MacCreary (1940, p. 11) mentions an anomalous form of *flavida* being more common than typical *flavida* in Delaware.

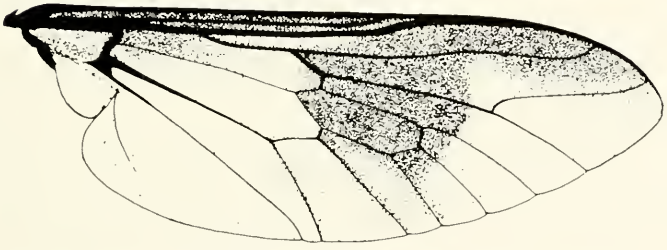
Pechuman (1949) distinguished *atlanticus* from *brunneus* in that *brunneus* has the first two antennal segments more swollen and the abdomen uniformly brown with occasional faint dark markings. Among other



41 abatus

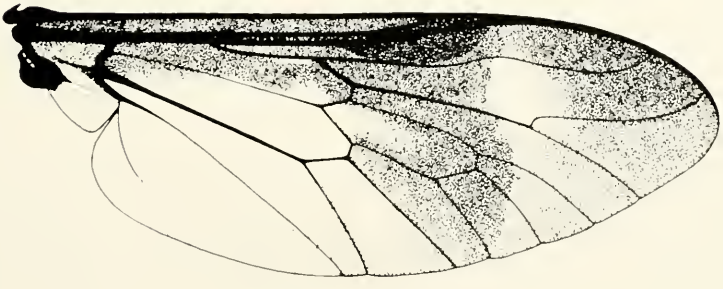


42 amazon hubbelli



43 atlanticus

44 beameri



45 bistellatus

Figures 41–45. Wing patterns of female *Chrysops*.

characters, he mentioned that the frontal callosity in *brunneus* usually is more protuberant and the wing pattern is a deeper color with the hyaline areas of the membrane lacking the yellowish tinge found in *atlanticus*. He stated that *atlanticus* differs from *flavidus* and its subspecies (now elevated to the rank of species) in that *flavidus* usually has the first two antennal segments more slender, the abdomen pale yellowish brown with faint brown markings, and the wing pattern distinctly outlined.

Pechuman also mentioned that specimens included in what is called *flavidus* show great variation and seem to form local races. He discussed a long series of the *flavidus* complex from southern Florida which have antennae much like *brunneus* but wing and body patterns close to *flavidus*. Another series of the *flavidus* form along the coast of the Carolinas, Georgia, and Florida have infuscated wing membranes but are separated from *atlanticus* by the brown thorax and different body coloration which frequently resembles *brunneus*.

Some specimens collected from the Mississippi Gulf coast during the present study resemble *flavidus* with the first and second antennal segments slender and abdomen a pale yellowish brown; however, a faint grayish blue-green cast is present on the anterior dorsum of the thorax, and the wing pattern is not distinctly outlined but faintly infuscated much like that of *atlanticus*. In addition, a series of specimens from the coastal marshes of Mississippi and Louisiana includes both "typical" *brunneus* and *atlanticus*, as well as intermediate forms. Most were collected flying together at many of the locations sampled including two inland sites in the longleaf-slash pine forests of Tangipahoa and St. Tammany parishes.

Pechuman (personal correspondence) would tend to limit the distribution of *atlanticus* to the Atlantic coastal states. Therefore, it is possible that the Mississippi and Louisiana specimens of *atlanticus* may represent an undescribed species, or be variants of *brunneus* or *flavidus*. I prefer to consider these specimens as geographic variants of the more eastern *atlanticus*. While it is possible to readily distinguish "typical" *atlanticus* from *brunneus*, and these in turn from "typical" *flavidus* by color and morphological characters, the variability and degree of intergradation between members of this complex indicate that the true relationships among these forms are yet to be resolved.

Ecology and Distribution: (April–September) *C. atlanticus* was collected from the coastal marshes and adjacent longleaf-slash pine forests. This species and *C. brunneus* are the major pest *Chrysops* near coastal regions.

Chrysops beameri Brennan, 1935
(Fig. 44)

Length 8 mm; mesonotum greenish yellow with dark stripes; abdomen yellow with four complete black stripes; apex of hyaline triangle extending above wing vein R_{2+3}.

Variations: (Specimens examined—2) Both agree with Brennan's (1935) description. Specimens of *C. beameri* are often difficult to separate from *C. hinei* Daecke and *C. sequax* Williston. Watson (1968) listed all three species from Alabama, and stated that key characters are insufficient to separate all specimens. He further indicated that the Alabama specimens determined as *sequax, beameri*, and *hinei* may have merely represented variation between local populations of the same species.

Ecology and Distribution: (June) One specimen was collected in Louisiana from a mixed pine-hardwood forest in Natchitoches Parish.

Chrysops bistellatus Daecke, 1905
(Fig. 45)

Length 7–11 mm; dorsum of thorax greenish gray with dark brown stripes; abdomen yellow with two submedian dark stripes; hyaline triangle of wing represented by an isolated spot in cell R_3.

Variations: (Specimens examined—147) Departures from Brennan's (1935) description include the following: palpi usually fuscous.

Ecology and Distribution: (April–June) This species was collected from the mixed pine-hardwood forests throughout the state and from the longleaf-slash pine regions of Tangipahoa and Washington parishes. Hine (1907a) reported this from Beauregard Parish.

Chrysops brimleyi Hine, 1904
(Fig. 46)

Length 6–9 mm; blackish; dorsum of thorax and abdomen with faint gray pubescence; apical spot of wing narrow; faint spot at furcation.

Variations: (Specimens examined—69) All specimens vary from Brennan's (1935) description in the following characters: frontal callus, lateral projections of frontoclypeus, lower margins of genae, palpi, black. Variations occasionally encountered include antennae dark brown to black with only basal ½ of scape yellowish; legs black. Two specimens taken in Rapides Parish have a broad apical spot entering the upper ¼ of cell R_4. In coastal areas, *C. brimleyi* may be confused with *C. fuliginosus*, but the latter is usually distinguished by having a more extensive apical spot and outer margin of crossband strongly bowed.

Ecology and Distribution: (March–May) This early season species was collected primarily from the mixed pine-hardwood forests of Rapides, St. Helena, and Union parishes. It was also taken from the longleaf-slash pine region of St. Tammany Parish and the upland hardwood area of West Feliciana Parish.

Mature larva (Fig. 11): Approximately 13–15 mm long; pubescence extremely pale to light brown, darkest on anal segment.

Head capsule length: 1.6 mm.

Striations: Encircling all segments, extremely fine and inconspicuous laterally on abdominal segments 2–7, in front of pseudopods, and on the anterior portion of anal segment.

Thorax: Anterior pubescent annuli faint, extending laterally approximately ⅔, ½, and ¼ the length of the pro-, meso-, and metathorax, respectively.

Abdominal segments 1–7: Anterior pubescence extremely faint and inconspicuous, encircling segments 1–4, progressively reduced on remaining segments. Pseudopodial pubescent rings complete on segments 1–4, joined with anterior pubescence dorsolaterally on segments 2–5 and ventrolaterally on 1–5. Posterior pubescence limited to a band encircling the preanal segment.

Anal segment: Pubescence consisting of a broad band encircling approximately the middle ½ of the segment, its anterior margin irregular with a prominent dorsolateral thumb-like projection and a shorter less conspicuous lateral projection. Additional pubescence consists of a conspicuous isolated spot somewhat anterior and ventral to the thumb-like projection and one or two small spots located near the segmental line.

Respiratory siphon: 0.71–0.76 mm long, approximately four times its basal diameter.

Comments: The description is based on two larvae from northwest Florida. They were collected from the margin of a lake in a longleaf-slash pine forest.

Chrysops brunneus Hine, 1903
(Fig. 47)

Length 8–12 mm; orange-brown; first two antennal segments swollen; wing mostly infuscated with clear areas anterior and posterior to crossband.

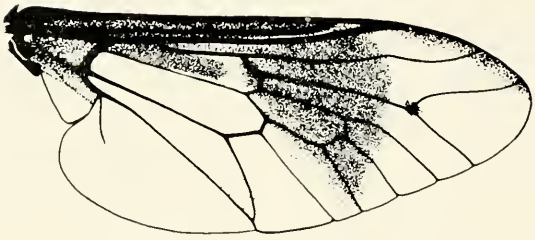
Variations: (Specimens examined—109) Most specimens agree with Hine's (1903) and Brennan's (1935) descriptions. They are separated from *C. atlanticus* by the characters listed by Pechuman (1949) (see discussion under *C. atlanticus*).

Ecology and Distribution: (April–September) This species was common along the coastal marshes and frequently was taken inland in the adjacent longleaf-slash pine forests of Florida, Alabama, Mississippi, and Louisiana. Hine (1907a) reported this species from the coastal marshes of Cameron and Plaquemines parishes and indicated that it was persistent and abundant throughout the day.

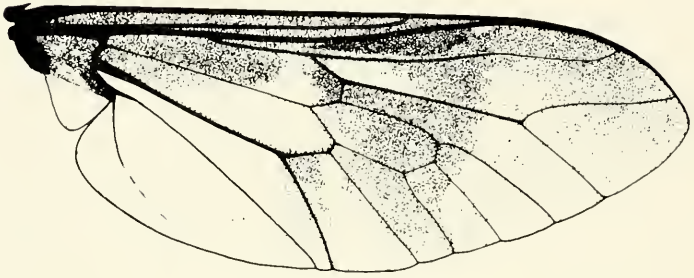
Chrysops callidus Osten Sacken, 1875
(Fig. 48)

Length 7–10 mm; dorsum of abdomen black with a median row of yellow triangles; lateral areas of tergites one and two and posterior margins of tergites, yellow; apical spot of wing narrow; both basal cells of female mostly hyaline.

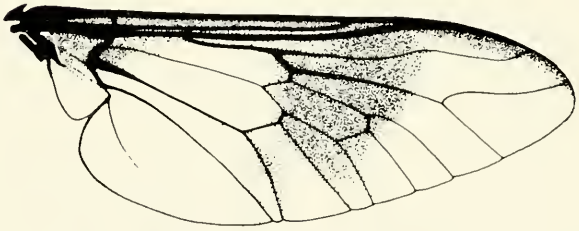
Variations: (Specimens examined—121) Departures from Brennan's (1935) description include the following: occasionally, legs yellow to dark brown lacking the typical black coloration; some specimens with basal ⅔ of fore femora and entire fore tibiae yellow-brown. Superficially this species re-



46 brimleyi

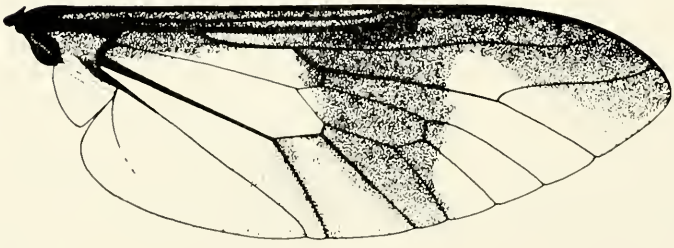


47 brunneus



48 callidus

49 carbonarius



50 celatus

Figures 46–50. Wing patterns of female *Chrysops*.

sembles *C. dimmocki* Hine and *C. pudicus* O.S., but can be separated from them by characters given in the key.

Ecology and Distribution: (March–September) This species was collected in all major vegetational regions except the coastal marsh. Although specimens were taken throughout the fly season, it was most abundant during April and May and was in many areas the most commonly collected species. On several occasions, it was observed feeding on female red-eared turtles (*Pseudemys scripta elegans*). Hine (1907a) noted *C. callidus* as an important livestock pest during the spring.

Mature larva (Fig. 21): 15–17 mm long; creamy white with pale golden brown pubescent markings.

Striations: Encircling all segments, somewhat closer together laterally.

Thorax: Anterior pubescent annuli narrow with thin lateral projections extending approximately ½ the length of the pro- and mesothorax, and ⅓ the length of the metathorax.

Abdominal segments 1–7: Anterior pubescence broadly encircling segments 1–3, reduced laterally on four, absent laterally on five or 6–7. Pseudopodial pubescent rings complete and joined with anterior pubescence dorso- and ventrolaterally on all segments. Posterior pubescence consists of a small midlateral pointed projection on the preanal segment.

Anal segment: Pubescence encircling segment excluding a median dorsal clear window and a lateral to ventral anterior clear area, the former (dorsal) portion occupying from ¼ to ⅓ the length of the segment, the latter sometimes considerably reduced. Scattered patches of anterior pubescence lie immediately adjacent to the segmental line.

Respiratory siphon: 0.46–0.55 mm, slightly longer than its basal diameter and possessing a stigmatal spine.

Comments: Eighteen larvae were collected from East Baton Rouge, East Feliciana, and St. Landry parishes. They were associated with aquatic habitats in mixed pine-hardwood and mixed bottomland hardwood forests. Most larvae were collected from the margins of small ponds or lakes and were seldom more than a few centimeters from the water. Some specimens taken during the winter months were collected at the bottom of ponds as far as ten meters from the shore and one meter beneath the water's surface. Jones and Bradley (1923) reared this species from a larva taken in mud at the bottom of a small brook.

Chrysops carbonarius Walker, 1848
(Fig. 49)

Length 7–9 mm; black; face with a median pollinose stripe; apical spot absent; cell Cu_1 with basal hyaline lunule.

Variations: (Specimens examined—13) All agree with Brennan's (1935) description.

Ecology and Distribution: (April–May) Specimens were collected in the upland hardwood forests of West Feliciana Parish, from the mixed pine-hardwood forests of Rapides Parish, and from the longleaf-slash pine region of Washington Parish. This early season species was seldom taken throughout the southeastern states.

Chrysops celatus Pechuman, 1949
(Fig. 50)

Length 7–9 mm; dorsum of thorax bluish green at least anteriorly, with dark stripes; abdomen yellowish with brown pattern.

Variations: (Specimens examined—127) In general the specimens agree with Pechuman's (1949) description for *C. flavidus celatus*. Variations include the reduction in size and darkening of the antennal segments becoming more *flavidus*-like in appearance, a reduction in the bluish green color of the thorax, leg color dirty yellow to fuscous with the apices of the fore and hind femora and tibiae dark, and wings faintly infuscated posteriorly.

Chrysops celatus is separated from *flavidus* by its grayish blue-green color on the mesonotum. However, intermediate forms exist in which the bluish color is extremely faint, and these specimens tend to approach *flavidus* in appearance. Teskey (1969) reared a larva of *flavidus* and 14 larvae of *celatus*, and on the basis of the differences of the larvae and pupae of these 2 forms considered *celatus* a distinct species.

During the present study 11 larvae of

celatus and 34 of *flavidus* were reared. While they were quite similar, *celatus* could usually be distinguished by its overall darker pubescence, the presence of posterior pubescence on abdominal segment 6, and the almost entirely pubescent anal segment. It is possible that the coincident separation of the larvae and the adults may be an example of concordant variation between the larval stage and the adult, and may not necessarily indicate two distinct populations.

Ecology and Distribution: (April–August) *C. celatus* was collected from the longleaf pine forests of St. Tammany, Rapides, Washington, and Winn parishes.

Mature larva (Fig. 17): 13–16 mm long; with light to medium golden brown pubescent markings.

Head capsule length: 1.5–1.6 mm.

Striations: Encircling all segments, somewhat closer together laterally.

Thorax: Prothoracic pubescent annulus with a lateral bib on each side extending approximately ½ the length of the segment; meso- and metathoracic annuli with lateral projections extending approximately ⅓ and ¼ the length of the segments, respectively.

Abdominal segments 1–7: Anterior pubescence encircling segments 1–5 to 7, reduced laterally on at least 6 and 7. Pseudopodial pubescence complete and joined with anterior pubescence dorso- and ventrolaterally on segments 2–7 and 1–7, respectively. Posterior pubescence present on segments 5 or 6–7, varying from a faint lateral trace when present on 5 to a distinct band encircling 7.

Anal segment: Pubescence extensive, covering almost the entire segment; hyaline portions include a narrow anterior area varying in extent from a thin line to approximately ⅛ the length of the segment, and one to several ventrolateral clear windows varying in size and situated posterior to the anus.

Respiratory siphon: 0.46–0.55 mm long, approximately 1.5 times its basal diameter and possessing a stigmatal spine.

Comments: The description is based on 11 larvae collected in northwest Florida. All were taken from a lake's margin in a longleaf-slash pine forest region.

Chrysops cincticornis Walker, 1848
(Fig. 51)

Chrysops celer Osten Sacken. Brennan, 1935, Kans. Univ. Sci. Bull. Vol. 22, p. 275.

Length 8–12 mm; black; face with a median pollinose stripe; pleura of female with dense orange pile; apical spot of wing absent.

Variations: (Specimens examined—36) Departures from Brennan's (1935) description include the following: usually scape of antenna yellowish brown, remainder dark brown to black; considerable variation in the extent of wing infuscation in the anal area, varying from almost clear with only a trace of infuscation along distal portion of vein $Cu_2 + 2A$, to almost entirely smoky. In the latter case, these specimens would fit the description (Fairchild, 1937) of *C. cincticornis* var. *nigroptera*. The writer has not seen type specimens of this form but feels that its status may be in question. The tendency of the wings to be folded over the abdomen in most pinned specimens helps to conceal any infuscation in the anal areas. In specimens from Louisiana, Alabama, and North Carolina, varying degrees of infuscation were observed when the wings were extended.

C. cincticornis resembles *C. carbonarius* Wlk., but the former can be distinguished by the complete infuscation of cell Cu_1 basally and also in the female the presence of dense orange pile on the thoracic pleura.

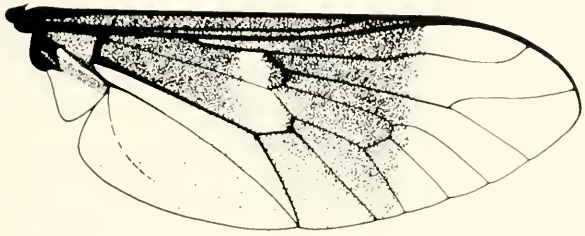
Ecology and Distribution: (April–May) This early season species was collected in the mixed pine-hardwood forests of East Feliciana, Rapides, and St. Helena parishes, and in the longleaf-slash pine forests of Tangipahoa, Vernon, and Washington parishes.

Mature larva (Fig. 22): 18 mm long; creamy white with pale to light golden brown pubescent markings.

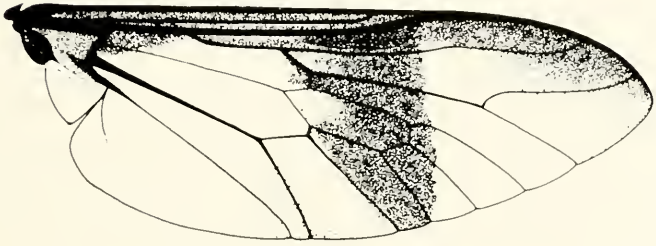
Head capsule length: 1.9 mm.

Striations: Encircling all segments, slightly closer together laterally.

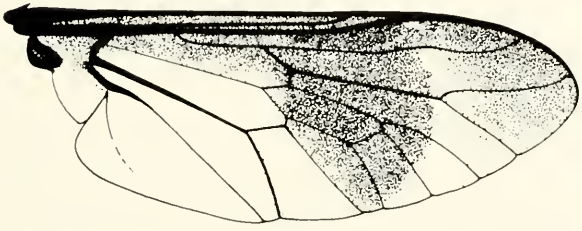
Thorax: Anterior pubescent annuli narrow with thin faint lateral projections extending at least ½, ⅓, and ¼, the length of the pro-, meso-, and metathorax, respectively.



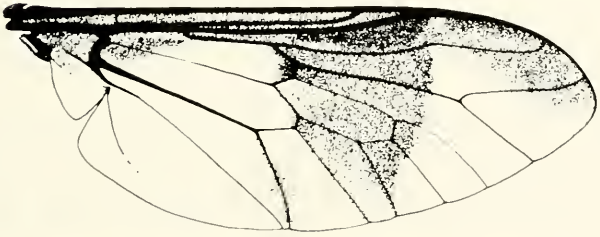
51 cincticornis



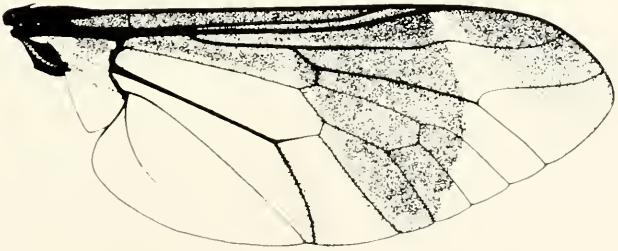
52 cursim



53 dacne



54 dimmocki



55 dorsovittatus

Figures 51–55. Wing patterns of female *Chrysops*.

Abdominal segments 1–7: Anterior pubescence encircling segments one and two, narrowly connected laterally on two; absent laterally on remaining segments. Pseudopodial pubescent rings complete and joined with anterior pubescence dorso- and ventrolaterally on segments 2–7 and 1–6, respectively. Posterior pubescence limited to a band encircling the preanal segment.

Anal segment: A wide pubescent band encircles the segment posteriorly covering less than ½ of the dorsal aspect; laterally the pubescent pattern curves somewhat anteriorly and extends ventrally in front of the anus. Two rounded pubescent spots and a narrow anterior band are situated dorsolaterally, the latter traversing the dorsum. A small isolated clear window lies ventrolaterally in the posterior pubescence.

Respiratory siphon: 0.6 mm long, approximately equal to its basal diameter and possessing a stigmatal spine.

Comments: The description is based on one larva taken from the margin of a small stream in Lee County, Alabama (upland hardwood area). Additional larvae from Alabama were collected from the margin of a small farm pond in a loblolly-shortleaf pine forest.

Chrysops cursim Whitney, 1879
(Fig. 52)

Length 7–9 mm; thorax greenish gray dorsally with dark stripes; abdomen yellow with an inverted V-shaped marking on tergite two, remaining segments with anterior emarginate black bands.

Variations: (Specimens examined—3) All differ from Brennan's (1935) description in the following: apical ¾ of fore tibiae and ½ of hind tibiae, black; crossband dark.

Ecology and Distribution: (May) Three specimens were collected from a longleaf-slash pine region in Washington Parish.

Chrysops dacne Philip, 1955
(Fig. 53)

Length 6–8 mm; brownish black; median portion of mesonotum bluish green; abdomen usually with faint suggestions of one or three pale stripes; apical spot of wing extensive.

Variations: (Specimens examined—34) Only one specimen was collected in Louisiana. It varies from Philip's (1955) descripas follows: apex of hyaline triangle extending to vein R_{2+3}; apices of hind tibiae and entire abdomen except a faint trace of a dorsal median line, fuscous.

Specimens collected in Alabama and Florida, do not always have the abdominal pattern present and show intergradation in characters with *C. parvulus* Daecke. Some of these intermediates have a much darker abdomen and more fuscous hind femora and tibiae like those of *parvulus*. The degree of infuscation in cells R_4 and R_5 varies considerably. Further information may indicate that these two forms are actually members of the same species as also suggested by Philip (1955). (For additional comments, see *C. parvulus*.)

Ecology and Distribution: (June) The single Louisiana specimen was collected in an upland hardwood forest in West Feliciana Parish. Specimens were also taken from longleaf-slash pine forests of Alabama and Florida (May–August). Hine's (1907a) description and locality data (northwest La.) for *C. lugens* would indicate that he probably had *C. dacne* and *C. parvulus* before him.

Chrysops dimmocki Hine, 1905
(Fig. 54)

Length 7–10 mm; abdomen black with a median row of small yellow triangles; lateral areas of tergites one and two, and posterior margins of tergites, yellow; apical spot of wing widened.

Variations: (Specimens examined—149) Departures from Brennan's (1935) description include the following: more uniformly darkened hind femora and tibiae; palpi dark brown to black; apex of hyaline triangle sometimes reaching wing vein R_{2+3}; number of black spots on abdominal venter usually reduced; black spot on tergite 2 not always attaining anterior margin.

C. dimmocki closely resembles *C. callidus* O.S., but the former can easily be separated by the greater extent of the apical spot. Several specimens from Vermilion and Tangipahoa parishes and Hancock County, Mississippi, show intergradation with *C. pudicus* O.S. These specimens have the apex

of the hyaline triangle just reaching vein R_{2+3} and the black spot on tergite two not reaching anterior margin, but in other characters they resemble *C. dimmocki*.

Ecology and Distribution: (March–June) This species was taken commonly along marshes of the mixed bottomland hardwood forests and occasionally from pine forests adjacent to the riverbottom swamps. It was collected from Ascension, Iberville, Livingston, St. Tammany, Tangipahoa, and Vermilion parishes.

Mature larva (Fig. 20): 14–18 mm long; creamy white with extremely pale to light brown pubescent markings.

Head capsule length: 1.6–1.8 mm.

Striations: Encircling all segments, somewhat closer together laterally.

Thorax: Anterior pubescent annuli with lateral projections extending approximately ⅔, ½, and ⅓, the length of the pro-, meso-, and metathorax, respectively.

Abdominal segments 1–7: Anterior pubescence encircling segments 1–4; narrowly connected laterally on 4; absent laterally on remaining segments. Pseudopodial pubescent rings complete and joined to anterior pubescence dorso- and ventrolaterally on segments 1–7. Posterior pubescence consists of a broad band encircling the preanal segment, a faint band encircling segment six and occasionally faint lateral traces on five.

Anal segment: Posterior pubescence encircling segment, covering at least ½ its length, enclosing the anus ventrally. A rather prominent dorsolateral thumb-like projection extends from the anterior margin of the posterior ring. Anterior pubescence consists of a narrow irregular lateral band.

Respiratory siphon: 0.46–0.58 mm, slightly longer than its basal diameter and possessing a stigmatal spine.

Comments: Numerous larvae were collected in Livingston Parish, in moist organic muck at the bases of gum trees in a tupelo gum-cypress swamp. Immediately adjacent to the swamp was an extensive cattail marsh. A single larva was collected from a rice field levee in the prairie region of Acadia Parish.

Chrysops flavidus Wiedemann, 1821
(Fig. 56)

Length 7–11 mm; yellowish with brown thoracic stripes and abdominal pattern.

Variations: (Specimens examined—380) In general the specimens agree with Brennan's (1935) description, omitting the key characters listed herein for *C. atlanticus, C. celatus*, and *C. reicherti. Chrysops flavidus* usually can be separated from these closely related species by using the following characters: first and second antennal segments slender, mesonotum yellowish with brown stripes, abdomen pale yellowish brown with faint brown markings, wing pattern distinctly outlined, and outer margin of crossband not sinuate. For comments concerning intermediates of the *C. flavidus* complex, see discussions under *C. atlanticus* and *C. celatus*.

Ecology and Distribution: (March–October) *C. flavidus* was one of the most commonly collected deer flies throughout the state. It was found in all major vegetational divisions, being most common in the swamps of the mixed bottomland hardwood regions. Hine (1906, 1907a) described this species as one of the worst stock pests in Louisiana although he may have been referring to other members of the complex as well.

Mature larva (Fig. 18): 15–17 mm long; creamy white with very pale to light golden brown pubescent markings.

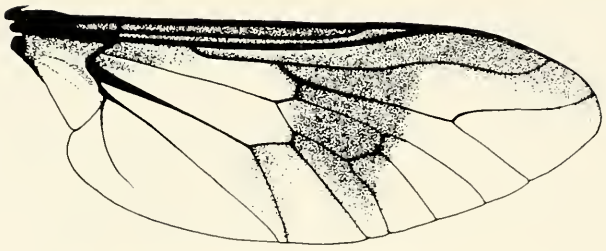
Head capsule length: 1.5–1.6 mm.

Striations: Encircling all segments, somewhat closer together laterally.

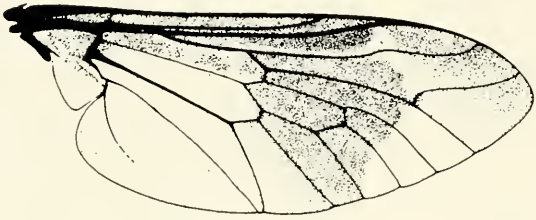
Thorax: Anterior pubescent annuli with a lateral prothoracic pubescent bib and lateral mesothoracic projections extending approximately ½ the length of the segments; lateral projections of metathorax poorly developed.

Abdominal segments 1–7: Anterior pubescence encircling segments 1–4 or 5, absent laterally on 6 and 7. Pseudopodial pubescent rings complete and joined with anterior pubescence dorso- and ventrolaterally. Posterior pubescence limited to a band usually completely encircling the preanal segment.

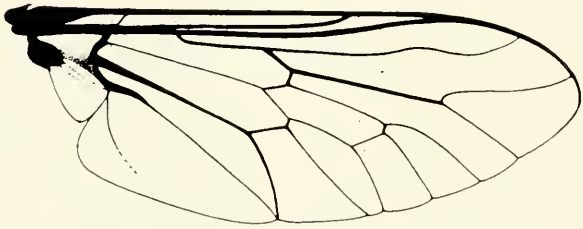
Anal segment: Posterior pubescence encircling the segment, covering approxi-



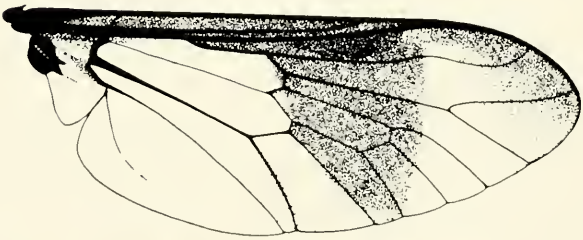
56 flavidus



57 fuliginosus



58 fulvistigma



59 geminatus

60 harmani

Figures 56–60. Wing patterns of female *Chrysops*.

mately ⅔ of the dorsal aspect; dorsolaterally the pubescence curves and widens extending short anteriorly directed projections; ventrally the pubescence encloses the anus. Anterior pubescence consists of a dorsal to dorsolateral band frequently joined with projections of the posterior pubescence; generally, two small inconspicuous pubescent spots are visible in the anterior ventrolateral clear area.

Respiratory siphon: 0.38–0.55 mm, slightly longer than its basal diameter and possessing a stigmatal spine.

Comments: Numerous larvae were collected throughout the state. In general they were more frequently taken at the margins of ponds and waterways in the mixed bottomland hardwood forests than in the other forest divisions of the state. Jones and Bradley (1923) reared a single larva taken from the bottom of a small brook.

Chrysops fulvistigma Hine, 1904
(Fig. 58)

Chrysops fulvistigma Hine, 1904, Can. Entomol. 36: 55; cotypes females, Raleigh, N.C.; Ohio State Univ. Brennan, 1935, Univ. Kans. Sci. Bull. 22: 300. Philip, 1947, Amer. Midland Natur. 37: 274.

Chrysops fulvistigma var. *dorsopuncta* Fairchild, 1937, Fla. Entomol. 19: 59; female, Lloyd, Jefferson Co., Fla. Philip, 1947, Amer. Midland Natur. 37: 274. (New Synonymy)

Length 6–8 mm; blackish; first two abdominal segments mostly yellow with median black markings; wing pattern usually extremely faint.

Variations: (Specimens examined—110) Occasional departures from Brennan's (1935) description include the following: a short midfacial pollinose stripe; faint apical wing spot; a dark infuscated crossband, the latter being quite distinct from the typical form. Hine (1907a, p. 30) also listed this variation, but it was apparently overlooked by Brennan. Some specimens have the second abdominal tergite with a single black median triangular or rectangular spot, or variation thereof. Hine's (1907a) description of *C. fulvistigma* from Louisiana included a large median black triangle on the second abdominal tergite. This and the dark crossband were the only features that varied from his original description (1904). In the abdominal characters, these specimens would fit the description of Fairchild (1937) for *C. fulvistigma dorsopunctus*.

In a series of over 100 specimens, of which approximately 25 percent were the *dorsopunctus* form, certain individuals exhibit intergradation in characters of the two forms. The black markings on abdominal tergite two show complete development from two small dashes to a single broad spot joined to the black marking of tergite one. Specimens representing *fulvistigma*, *fulvistigma dorsopunctus*, and intermediates all have partial midfacial pollinose stripes, and members of both forms and intermediates exhibit the presence of a saturate crossband. These specimens were collected together in Natchitoches, Rapides, St. Tammany, and Tangipahoa parishes. Based on the above information, I consider both forms as a single taxon.

Ecology and Distribution: (May–August) This species was collected from the longleaf-slash pine forests and mixed pine-hardwood forests of southeastern Louisiana. Specimens were also taken from similar forest types in Natchitoches, Rapides, and Winn parishes. Jones and Bradley (1924) reported this species in the vicinity of Baton Rouge.

Chrysops geminatus geminatus Wiedemann, 1828
(Fig. 59)

Length 6–8 mm; thorax grayish yellow with dark stripes; abdomen yellow with black pattern, second tergite with two oblique spots; apex of hyaline triangle extending well beyond vein R_{2+3}.

Variations: (Specimens examined —62) Departures from Brennan's (1935) description include the following: occasionally pedicel and entire third antennal segment black; a few specimens have fore femora brown, entire tibiae black, entire middle femora, proximal and distal portions of middle tibiae, black; occasionally inverted V of tergite two reaching hind margin.

Ecology and Distribution: (May–July) *C. geminatus geminatus* was collected in the longleaf-slash pine and the mixed pine-

hardwood forests of Beauregard, East Feliciana, Rapides, St. Tammany, and Washington parishes.

Chrysops geminatus impunctus Krober, 1926
(Fig. 59)

Length 6–8 mm; thorax grayish yellow with dark stripes; first and second abdominal segments yellow, last three segments mostly black; apex of hyaline triangle extending well beyond vein R_{2+3}.

Variations: (Specimens examined—14) Departures from Brennan's (1935) description include the following: occasionally faint submedian dark dashes anteriorly directed from the posterior margin of tergite two; intermediate conditions in leg coloration approaching that of *geminatus geminatus*.

Application of the subspecific category is questionable as applied to *C. geminatus impunctus*. Both forms were found in the same general regions; however, unlike both forms of *C. fulvistigma*, the two forms of *C. geminatus* were seldom collected together during the present investigation. The *impunctus* specimens are rarely collected and may simply represent a genetic variant of *geminatus*. The possibility also exists that the two forms may actually represent distinct species; however, additional information is needed to clarify the relationship between them.

Ecology and Distribution: (May–July) *C. geminatus impunctus* was taken in the upland hardwood forests of West Feliciana Parish.

Chrysops ***harmani*** n. sp.
(Figs. 9, 10, 60)

Holotype female, 7mm. Antennae normal, first segment yellow, second brownish, third dark brown to black with basal portion somewhat lighter. Frons with grayish yellow pollen; frontal callosity black, somewhat broader than tall. Ocellar area black with some yellowish gray pollen. Area around base of antennae and sides of face with golden yellow pollen, a short pollinose spur extending obliquely below each antenna on the frontoclypeus. Frontoclypeus mostly black with a narrow median yellowish brown area. Lower genae black. Palpi brownish.

Dorsum of thorax dark with grayish green pollen and five dark stripes, the median one narrow. A yellowish gray stripe is present above wing base. Scutellum black with some grayish green pollen. Pleura with two grayish yellow stripes on black background. Fore coxae, most of fore femora, and base of tibiae, yellow; extreme apical portion of fore femora, apical ¾ of tibiae and entire tarsi, dark brown to black. Middle and hind femora ½ and completely black, respectively. Middle tibiae and first two tarsal segments yellowish, remaining tarsal segments darker. Hind tibiae yellowish except for extreme apical portions which are black; first tarsal segment yellow, remaining tarsal segments darker.

Wing with crossband complete to hind margin. Apical spot fading posteriorly in cell R_4. First basal cell mostly infuscated with an apical hyaline area not clearly crossing the cell.

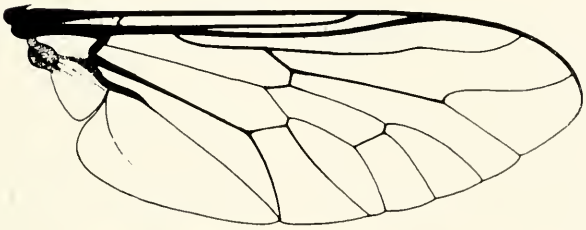
Abdomen yellow and black with a broad mid-dorsal black band the length of the abdomen; this band with faint indications of a median dorsal yellow stripe on segments three and four. A sublateral black band extends posteriorly on each side from tergite three, widening progressively caudally. Apical portion of abdomen dark brown to black. Venter yellow with a pronounced median dark brown band attenuated anteriorly, terminating with an isolated spot on sternite two. Dark lateral bands extend from segment two posteriorly.

From a mixed pine-hardwood region of St. Helena Parish, La., La. 1045, 13 May 1970 (Mac Tidwell). Holotype in the National Museum of Natural History, No. 72107.

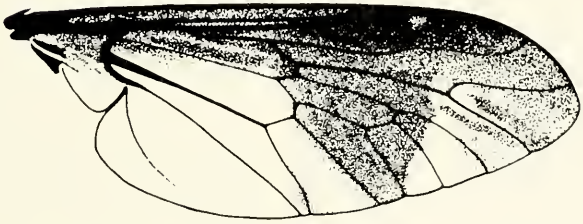
This species has affinities with and would key out to *C. pikei* Whit. in Philip's (1955) *Chrysops* key. It is separated from *pikei* by the presence of a mid-dorsal black stripe on the abdomen, the greater extent of the hyaline triangle crossing vein R_{2+3}, the less extensive apical spot, the frontoclypeus mostly black, and the overall darker color of the thorax.

The writer takes pleasure in naming this species after Dr. Walter J. Harman, Head, Department of Zoology and Physiology, Louisiana State University, who has so kindly provided encouragment and assistance throughout this study.

61 hinei

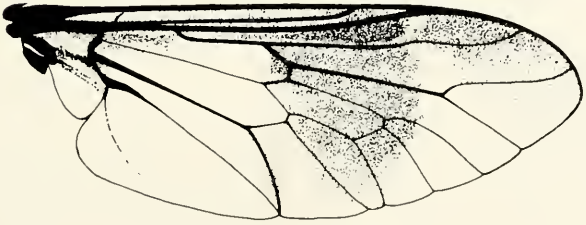


62 hyalinus



63 macquarti

64 moechus



65 montanus

Figures 61–65. Wing patterns of female *Chrysops*.

Chrysops macquarti Philip, 1961
(Fig. 63)

Chrysops univittatus of authors. Brennan, 1935, Kans. Univ. Sci. Bull. Vol. 22, p. 344.

Length 6–8 mm; thorax greenish gray above with dark stripes; abdomen yellow with two submedian dark lines expanding posteriorly; apical spot of wing extensive; apex of hyaline triangle usually attaining at least furcation.

Variations: (Specimens examined—55) In general the specimens agree with Brennan's (1935) description and Philip's (1961) variations. Variations noted in some Louisiana specimens include the following: palpi darkened; most of fore tibiae black, extreme basal portions lighter; two fuscous abdominal stripes extensive covering greater portion of dorsum; only first two abdominal segments with lateral margins yellow; entire venter fuscous except anterior lateral yellow areas. Some specimens of *C. macquarti* resemble *C. moechus* O.S., however, the former can be separated by its more extensive hyaline triangle.

Ecology and Distribution: (April–August) This species was collected primarily during May and June in the upland hardwood forests of West Feliciana Parish and from the longleaf-slash pine region in Washington Parish. One other specimen was taken in a mixed pine-hardwood forest of DeSoto Parish. The *C. univittatus* reported from Louisiana by Hine (1907a) was actually *C. macquarti*.

Chrysops moechus Osten Sacken, 1875
(Fig. 64)

Length 7–10 mm; mesonotum greenish gray with dark stripes; abdomen yellow, darker posteriorly usually with four black stripes; apical spot of wing extensive; hyaline triangle not exceeding vein M_1.

Variations: (Specimens examined—165) Departures from Brennan's (1935) description include the following: hyaline triangle sometimes slightly exceeding vein M_1; dorsum of abdomen often with two solid, rather than broken, black median stripes; broken black stripe on each side present or absent; venter with a median black stripe sometimes attaining the anterior abdominal margin; occasionally base of middle femora and entire hind femora except extreme apices, black. Certain of these characters may approach those of *C. macquarti* Phil. The extension of the hyaline triangle into cell R_5 is rarely observed in *moechus*, and specimens exhibiting this character usually lack the extensive darkening of the median dorsal abdominal lines posteriorly as found in *macquarti*.

Localized populations of *C. moechus* in St. Helena and East Feliciana parishes (37 specimens examined) have a characteristic appearance and exhibit the following characters either singly or in combination: hyaline areas present in cell R_5 which appear as an extension of the hyaline triangle; sublateral black abdominal stripes often reaching well into tergite one; basal portion of frontal callus frequently with yellowish shades; converging black markings on tergite two broadly joined to prominent spot beneath scutellum.

Ecology and Distribution: (April–August) This species was collected most often along streams or roads in thick wooded areas. It was taken in the mixed pine-hardwood forests of DeSoto, Natchitoches, St. Helena, St. Tammany, and East Feliciana parishes. Specimens were also taken from the upland hardwood region of West Feliciana Parish and from the longleaf-slash pine forests of Washington Parish. Hine (1907a) recorded this species from Sabine Parish.

Chrysops montanus Osten Sacken, 1875
(Fig. 65)

Length 7–10 mm; thorax grayish green with dark stripes; abdomen yellow and black, second tergite with two oblique dark spots; tergites 3–5 with four rows of black spots; apical spot broad filling at least ½ of cell R_4.

Variations: (Specimens examined—168) Departures from Brennan's (1935) description include the following: palpi variable, yellow to fuscous; frequently frontal callus black with yellowish brown maculations; median black spots on venter of abdominal segments may be absent; occasionally base of middle femora and basal ¾ or more of hind femora, black; apical ¼ of hind tibiae, fuscous. Variations rarely observed include first basal cell entirely infuscated; hyaline triangle reaching or crossing vein R_{2+3};

crossband terminating in cell M_3 and not crossing base of cell Cu_1. Specimens exhibiting the latter character together with infuscation of first basal cell may key to *C. striatus* O.S. in Philip's (1955) key to the *Chrysops*.

Ecology and Distribution: (April–July) This species was collected in the longleaf pine forests of Evangeline and Tangipahoa parishes, and from the mixed pine-hardwood forests of Claiborne, Rapides, and Winn parishes. Jones and Bradley (1923, 1924) reported this species from East Baton Rouge Parish.

Chrysops niger Macquart, 1838
(Fig. 66)

Length 6–9 mm; black; frontoclypeus yellow; wing hyaline beyond crossband.

Variations: (Specimens examined—18) Departures from Brennan's (1935) description include the following: first basal cell and sometimes costal cell may be almost completely hyaline with only a trace of infuscation; occasionally middle and hind metatarsi fuscous.

Ecology and Distribution: (April–May) This early season species was taken from the upland hardwood forests of West Feliciana Parish and the longleaf-slash pine region in Washington Parish. A single specimen was taken in the mixed bottomland hardwood region of Ascension Parish.

Mature larva (Fig. 15): 12–16 mm long; creamy white with extremely faint to moderately intense pubescent markings.

Head capsule length: 1.6–1.7 mm.

Striations: Encircling all segments, finer on prothorax and somewhat closer together laterally.

Thorax: Anterior pubescent annuli extremely faint extending approximately ¾, ⅓, and ¼, the length of the pro-, meso-, and metathorax, respectively; lateral projections absent.

Abdominal segments 1–7: Anterior pubescence limited to pale, inconspicuous and much reduced traces. Pseudopodial pubescent rings incomplete. Posterior pubescence limited to a small midlateral patch on the preanal segment.

Anal segment: A broad posterior pubescent band covers over ½ the length of the segment; its anterior border irregular with prominent rounded projections laterally and ventrolaterally; the clear area between the projections club-shaped with the head directed posteriorly; ventrally the pubescence encloses the anus. Anterior pubescence consists of a narrow irregular band. Dorsolaterally, a pubescent spot is situated in the clear area between the anterior and posterior rings.

Respiratory siphon: 0.50–0.53 mm, slightly longer than its basal diameter and possessing a stigmatal spine.

Comments: Eight larvae were collected from the margins of a small stream in the longleaf-slash pine region of Washington Parish, and one specimen was found at the margin of a small farm pond in a pine woods region of Alabama.

Chrysops nigribimbo Whitney, 1879
(Fig. 67)

Length 5–8 mm; black; wing pattern faint.

Variations: (Specimens examined—10) Departures from Brennan's (1935) description include the following: palpi variable, yellow to fuscous; pleurae shiny black with a pronounced ventrolateral white stripe, dorsolateral stripe inconspicuous.

Ecology and Distribution: (May) Five specimens were collected in a longleaf-slash pine forest in St. Tammany Parish. The forest was situated on a ridge overlooking a cypress swamp on the Pearl River. Five other specimens (northwest Florida) were collected in longleaf-slash pine forests immediately adjacent to small lowland swamps.

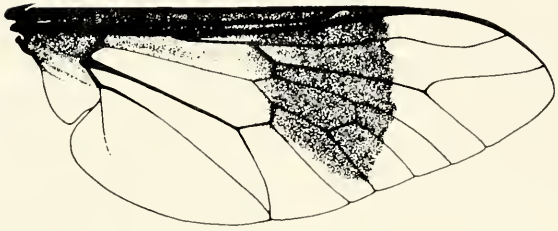
Mature larva (Fig. 14): Approximately 12 mm long, with extremely pale to light brown pubescent markings.

Head capsule length: 1.3–1.4 mm.

Striations: Encircling all segments, appearing prominent and irregular, somewhat more closely spaced laterally.

Thorax: Anterior pubescent annuli extending less than ¼ the length of the segments; only slight indications of lateral projections.

Abdominal segments 1–7: Anterior pubescence encircling segment one, reduced laterally; absent laterally and becoming progressively reduced ventrolaterally on 2–7. Pseudopodial pubescence complete on seg-

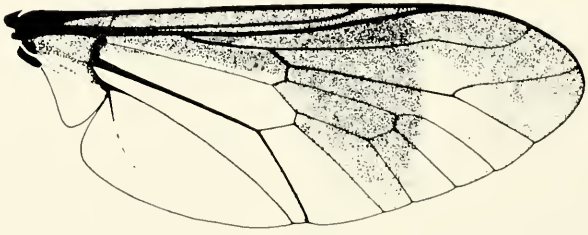


66 niger

67 nigribimbo

68 obsoletus

69 parvulus



70 pikei

Figures 66–70. Wing patterns of female *Chrysops*.

ments 1–4, joined with anterior pubescence dorsolaterally on 2–7 and ventrolaterally on segments 1–2 or 3. Posterior pubescence limited to a narrow band encircling the preanal segment.

Anal segment: Pubescent configuration irregular varying in intensity from faint to very light brown, covering most of the anterior aspects; posterior ventrolateral portion largely clear.

Respiratory siphon: Approximately 0.50 mm, slightly over twice its basal diameter.

Comments: The description is based on two larvae collected from a lake margin in northwest Florida (longleaf-slash pine forest region).

Chrysops obsoletus obsoletus Wiedemann, 1821
(Fig. 68)

Length 7–9 mm; blackish; yellow stripe on thorax above wing base; abdominal dorsum with three more or less obsolete yellow stripes; hyaline triangle extending to vein R_{2+3}; apical spot extensive; tinting in posterior region of wing often lighter than figured.

This form was not collected in Louisiana by the author. Hine's (1907a) description of *C. obsoletus* would indicate that his specimens were either *C. upsilon* Phil. or *C. univittatus* Macq. *Chrysops obsoletus* was also reported from the state by Jones and Bradley (1923, 1924), Wilson (1963), and Wilson and Burns (1964). Descriptive information for their specimens was not given. However, since *C. obsoletus* is a coastal species, the ecological information provided by both Jones and Bradley (1924) and Wilson (1963) would indicate that they were probably working with a different taxon.

Chrysops obsoletus lugens Wiedemann, 1821
(Fig. 68)

Chrysops ultima Whitney. Brennan, 1935, Kans. Univ. Sci. Bull. Vol. 22, p. 343.

Length 7–8 mm; blackish; yellow stripe on thorax above wing base; abdomen dark, occasionally with faint middorsal line; hyaline triangle extending to vein R_{2+3}; apical spot extensive; wing as figured, tinting in posterior region usually darker than in *C. obsoletus obsoletus*.

Variations: (Specimens examined—84) Departures from Brennan's (1935) description include the following: usually most of hind femora and occasionally entire fore and hind tibiae, fuscous; sometimes wing completely infuscated.

Ecology and Distribution: (June–August) *C. obsoletus lugans* was locally abundant in the longleaf-slash pine forests along the Gulf coast of Florida, Alabama, and Mississippi. In Louisiana it was collected in longleaf-slash pine forests adjacent to the coastal marsh in St. Tammany Parish.

Chrysops parvulus Daecke, 1907
(Fig. 69)

Length 6–8 mm; brownish black; median portion of mesonotum bluish green; apical spot of wing extensive.

Variations: (Specimens examined—7) Only one specimen was collected in Louisiana. In general the specimens agree with Brennan's (1935) description. *Chrysops parvulus* closely resembles *C. dacne* Phil., and intermediate specimens cannot be placed with certainty into either taxon. Watson (1968) collected both forms and intermediates in Alabama, and stated that there was almost complete intergradation between the two species as recognized during his study. (For further comments, see *C. dacne*.)

Ecology and Distribution: (June) The single Louisiana specimen was taken from a longleaf pine forest in Rapides Parish. Other specimens were collected in Alabama and Florida.

Chrysops pikei Whitney, 1904
(Fig. 70)

Length 6–9 mm; yellow and black; abdomen with 4 black stripes, the lateral ones shorter; apex of hyaline triangle terminating in wing cell R_3.

Variations: (Specimens examined—430) Departures from Brennan's (1935) description include the following: palpi tan to dark brown, frequently anterior reddish tan, posterior dark; base of hind femora black, sometimes extending the length of the segment; distal ⅔ of fore tibiae dark; usually scutellum entirely dark; in rare cases apex of hyaline triangle extending to vein R_{2+3};

occasionally hyaline triangle only just encompassing fork; midventral abdominal black spots sometimes absent; posterior lateral regions of the abdominal dorsum often completely fuscous, and rarely faint indications of lateral lines extending to base of abdomen.

Ecology and Distribution: (April–September) *C. pikei* was one of the most commonly collected deer flies. It was taken throughout the state from all major vegetational regions except the prairie and coastal marsh. Hine (1906, 1907a) reported this species a common pest in many portions of the state.

Mature larva (Fig. 12): 13–14 mm long; creamy white with very faint to moderately intense pubescent markings.

Head capsule length: 1.3–1.5 mm.

Striations: Encircling all segments, somewhat more closely spaced laterally.

Thorax: Anterior pubescent annuli extremely pale and inconspicuous, occupying approximately ⅔, ⅓, and ¼, the length of the pro-, meso-, and metathorax, respectively; lateral projections absent.

Abdominal segments 1–7: Anterior pubescence faint, encircling segment one; becoming progressively reduced laterally on remaining segments and ventrolaterally on six and seven. Pseudopodial pubescent rings complete and joined with anterior pubescence dorsolaterally on segments 1–7 and ventrolaterally on at least 1–5. Posterior pubescence limited to a narrow irregular band encircling the preanal segment.

Anal segment: Posterior pubescent ring distinct, covering approximately ½ the segment and fading posteriorly; dorsally its anterior border extends paired rounded projections; ventrally it encloses the anus. Anterior pubescence consists of pale dorsal and midlateral patches. A distinct isolated pubescent spot is situated dorsolaterally in the anterior clear area of the segment.

Respiratory siphon: Long and slender, 0.84–0.88 mm, approximately four times its basal diameter.

Comments: Four larvae were taken from debris in a narrow, sandy-bottom stream draining a mixed pine-hardwood forest in East Feliciana Parish. Jones and Bradley (1924) reared this species from a larva collected from the muddy margin of a stagnant pool in East Baton Rouge Parish.

Chrysops pudicus Osten Sacken, 1875 (Fig. 71)

Length 7–8.5 mm; thorax bluish gray with dark stripes; abdomen yellow with black pattern, inverted V of tergite two usually not reaching anterior margin of segment; apical spot slightly widened, usually including only apex of cell R_4; apex of hyaline triangle usually attaining vein R_{2+3}.

Variations: (Specimens examined—59) Departures from Brennan's (1935) description include the following: usually apex of fore femora, at least distal ½ of fore tibiae, and entire hind femora, black; rarely specimens with a more extensive apical spot like that of *C. dimmocki* Hine and hyaline triangle not reaching vein R_{2+3}. This species is close to *C. dimmocki* but can usually be separated by a combination of key characters. (See also under *C. dimmocki*.)

Ecology and Distribution: (May–August) Specimens were collected from the mixed pine-hardwood forests of Rapides Parish, and the longleaf-slash pine region of Tangipahoa and St. Tammany parishes. Hine (1907a) reported this species from DeSoto Parish.

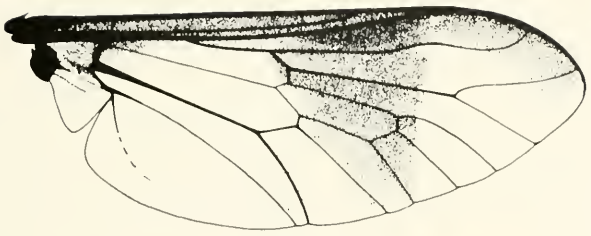
Chrysops reicherti Fairchild, 1937 (Fig. 72)

Chrysops reicherti Fairchild, 1937, Fla. Entomol. 19: 60–61.

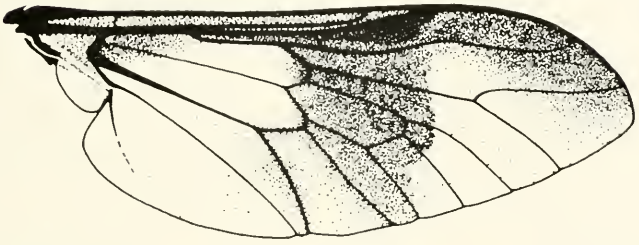
Chrysops flavida subsp. *reicherti* Fairchild. Philip, 1947, Amer. Midland Natur. 37: 273.

Length 7–11 mm; yellowish with brown thoracic stripes; base of abdomen with a pale greenish yellow color, remainder straw yellow to brown; outer margin of crossband sinuous; faint tinting in the usual hyaline areas along posterior wing margin.

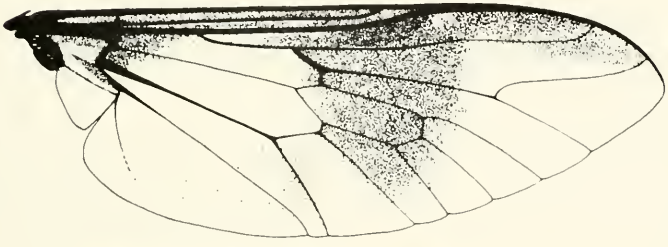
Variations: (Specimens examined—358) In general the specimens agree with Fairchild's (1937) description and are similar to a paratype supplied through the courtesy of Dr. L. L. Pechuman. Some observed variations include: wing tinting of usual hyaline



71 pudicus



72 reicherti



73 sackeni

74 separatus

75 sequax

Figures 71–75. Wing patterns of female *Chrysops*.

areas pale to dark; hind femora varying from dark brown to black; rarely second segment of abdomen straw yellow; and apical spot occasionally completely filling second submarginal cell.

Chrysops reicherti is separated from *C. flavidus* by its almost translucent greenish yellow color of the first and second abdominal segments, and the sinuous outer margin of the crossband. Even though the larvae of this species are similar to *flavidus*, the latter can be separated by the presence of a prothoracic pubescent bib and a posterior pubescent band on the preanal segment. Both *reicherti* and *flavidus* are sympatric throughout much of the Southeast, with *flavidus* extending a little more north and west than *reicherti*. Based on the distinctiveness of the larvae, and the present knowledge of adult morphology and distribution, I consider *C. reicherti* a distinct species and return it to specific rank.

Ecology and Distribution: (April–September) This species was taken throughout the state in all major vegetational regions, being most common in the swamps of the mixed bottomland hardwood forests.

Mature larva (Fig. 19): 16–18 mm, creamy white with pale to light brown pubescent markings.

Head capsule length: 1.6–1.7 mm.

Striations: Encircling all segments, somewhat more closely spaced laterally.

Thorax: Anterior pubescent annuli pale with lateral projections extending approximately ½ the length of the pro- and mesothorax, and ¼ the length of the metathorax.

Abdominal segments 1–7: Anterior pubescence encircling segments 1–3 or 4; absent laterally on remaining segments and progressively reduced ventrolaterally on 5–7. Pseudopodial pubescent rings complete and joined with anterior pubescence dorso- and ventrolaterally. Posterior pubescence, when present, limited to a tiny midlateral spot on the preanal segment.

Anal segment: Pubescence consisting of an irregular narrow anterior ring and a wide posterior ring encircling the segment, the latter occupying over ½ of the segment dorsally and joined dorsolaterally with the anterior pubescence; ventrally the posterior pubescence encloses the anus.

Respiratory siphon: 0.42–0.50 mm, slightly longer than its basal diameter and possessing a stigmatal spine.

Comments: Nine larvae were taken from several small ponds in a mixed bottomland hardwood forest and from the margin of a small lake in a cypress swamp. The collecting sites are located in St. Landry and St. Tammany parishes.

Chrysops separatus Hine, 1907
(Fig. 74)

Length 7–9 mm; black; face with median pollinose stripe; apical spot of wing separated from crossband.

Variations: (Specimens examined—3) In general all agree with Brennan's (1935) description with the exception that cell Cu_1 was not infuscated and the apical spot was somewhat reduced in two specimens.

Ecology and Distribution: (April) The author examined a single specimen collected by W. G. Bradley from East Baton Rouge Parish. Two other specimens were collected from Arkansas and Alabama in upland hardwood forests. A distinctive species but seldom collected—prior to the present investigation it was reported from Mississippi, North Carolina, Oklahoma, and Louisiana. Jones and Bradley (1923) reported a female of this species feeding on a cow in East Baton Rouge Parish.

Chrysops sequax Williston, 1887
(Fig. 75)

Length 8–9 mm; frontal callus black; mesonotum yellowish green with dark stripes; abdomen yellow with four complete black stripes; apical spot extensive filling apex of cell R_5 and occasionally entering cell M_1; apex of hyaline triangle extending above vein R_{2+3}.

Ecology and Distribution: This species was reported from Rapides Parish (August) by Hine (1907a). However, based on his description of *sequax* (p. 34), he apparently had specimens of *C. beameri* or a mixed population of both species before him (see also discussion under *C. beameri*). *C. sequax* was also recorded from Louisiana by Wilson and Burns (1964).

Chrysops striatus Osten Sacken, 1875
(Fig. 76)

Length 7–10 mm; frontal callosity usually black; abdomen yellow above with four black stripes, the lateral ones reduced; first basal cell infuscated; hyaline triangle not reaching vein R_{2+3}.

This species was reported from Louisiana by Philip (1947) and Wilson and Burns (1964). However, since the separation of *C. aberrans* Phil. from this complex, this southern extension of the range of *striatus* may be doubtful. Some variants of *C. montanus* with infuscated first basal cell and infuscation not crossing cell Cu_1, may key to *C. striatus* in Philip's (1955) key to the *Chrysops*.

Chrysops univittatus Macquart, 1855
(Fig. 78)

Length 6.0–8.5 mm; mesonotum dark greenish blue; abdomen brownish black with a middorsal yellow stripe; costal cell infuscated; apical spot variable, usually filling ½ or less of cell R_4, ocasionally nearly filling cell.

Variations: Resembling *C. upsilon* Phil., to be separated by characters discussed here and under *upsilon*. From four similar larvae collected during the present study, a male and female of *C. univittatus* and two males of *C. upsilon* were reared. Both of the *univittatus* specimens have a narrow apical spot and dark costal cell. In addition the male has a dark first basal cell and a small midfacial pollinose stripe extending about ¼ the distance to the oral margin. The two *upsilon* specimens have a light but broad apical spot invading cell R_5, costal and first basal cells infuscated. The midfacial pollinose stripe reaches the oral margin in one specimen, but in the other it extends approximately ½ the distance to oral margin.

These reared specimens were collected together from the same habitat and emerged within one week of each other. It is possible that both *C. univittatus* and *C. upsilon* were present in the same habitat and that their larvae are very similar. The possibility also exists that these two forms may not be distinct species; however, additional data is needed to confirm this.

The *C. univittatus* reported from the state by Hine (1907a) was actually *C. macquarti* Phil.

Mature larva (Fig. 16): 12–13 mm long; creamy white with light pubescent markings, darkest on anal segment.

Head capsule length: 1.4–1.5 mm.

Striations: Encircling all segments, somewhat more closely spaced laterally.

Thorax: Prothoracic annulus with a lateral pubescent bib extending about ½ the length of the segment; mesothoracic annulus with extremely short lateral pubescent projections; metathoracic annulus at most with only indications of lateral projections.

Abdominal segments 1–7: Anterior pubescence encircling segments 1–5 or 6, absent laterally on 7. Pseudopodial pubescent rings complete on all segments and joined with anterior pubescence dorso- and ventrolaterally. Posterior pubescence limited to a band encircling the preanal segment.

Anal segment: Posterior pubescence encircles the segment, covering about ½ of the dorsal aspect; the pubescence curves and widens covering over ¾ of the lateral aspects; the posterior pubescence forms a rather enlarged projection dorsolaterally, and ventrally encloses the anus; posteriorly the pubescence fades before reaching the siphon. Anterior pubescence consists of a spot or small projection located dorsally to dorsolaterally, and one to two spots located laterally to ventrolaterally.

Respiratory siphon: 0.53–0.56 mm, nearly 1.5 times its basal diameter and possessing a stigmatal spine.

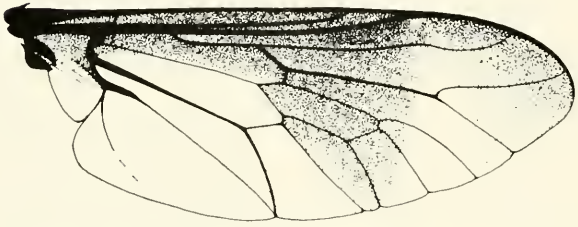
Comments: The larvae were taken from the margins of a small stream draining a longleaf-slash pine region in Washington Parish.

Chrysops upsilon Philip, 1949
(Fig. 79)

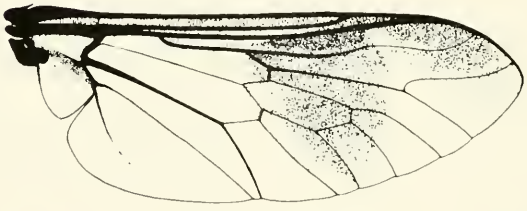
Length 7–9 mm; face with a median pollinose stripe; mesonotum dark blue-green; abdomen brownish black with a median yellow stripe; costal cell usually hyaline; apical spot broad, including most of cell R_4 and entering cell R_5.

Chrysops upsilon is frequently confused with *C. univittatus* Macq., and Philip (1949)

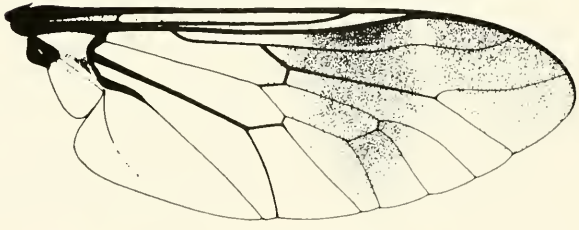
76 striatus



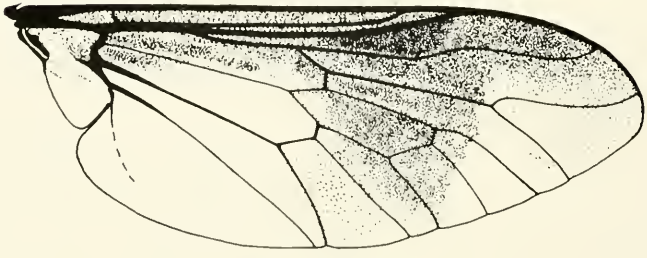
77 tidwelli



78 univittatus



79 upsilon



80 vittatus

Figures 76–80. Wing patterns of female *Chrysops*.

separates the former by the presence of an upsilon or T-shaped pollinose marking on the frontoclypeus beneath the antennae, a clear or lightly infuscated costal cell in the female, and a wider apical spot.

Variations: (Specimens examined—162) Departures from Philip's (1949) written description include the following: midfacial pollinose stripe varied in length, sometimes less than ⅓ the distance to oral margin in both sexes; basal ¾ of hind femora black; apical wing spot sometimes very faint; apex of hyaline triangle may extend to costal vein; usually first basal cell lightly infuscated; occasionally costal cell dark. Philip (p. 459) stated that *C. upsilon* had an almost hyaline costal cell although his wing figure shows a dark costal cell.

Male description: The male is herein described for the first time. Scape of antenna yellow, pedicel and base of flagellum brown, apex black. Palpi black. Face yellow, tubercles black and slightly swollen with a T-shaped yellow pollinose marking between them, the stem of which tapers and reaches the oral margin. Lateral areas of face with a band of yellow pollinose above cheeks. Lower margin of gena with a black spot. Dorsum of thorax fuscous with a broad median blue-green pollinose area concolorous with scutellum. Faint blue-green stripe above wing base, area between this and median stripe covered with golden reddish pollen. Pleura fuscous with two yellow pollinose stripes. Legs yellow, distal ½ of fore tibiae and entire tarsi black; basal ¼ and ½, respectively of middle and hind femora black; extreme apices of hind tibiae and apical tarsal segments of middle and hind tarsi, fuscous. Wing similar to female but with costal and first basal cells infuscated, and a streak in second basal cell reaching ¾ the length of the cell. Abdomen dark with a narrow yellow middorsal line extending to segment five; traces of submedian and lateral spots on segments 1–4. Venter of abdomen with a median fuscous stripe widening posteriorly; lateral areas of segments 1–3 yellow with the usual lateral stripes present.

The description is based on a specimen collected in St. Landry Parish, Louisiana, 2 July 1965. Variations observed in nine other Louisiana males are as follows: two specimens with the midfacial pollinose stripe extending approximately ½ the distance to oral margin, and in one of these, the infuscated streak in the second basal cell is considerably reduced and a faint infuscation is present in cell Cu_1.

The males of *C. upsilon* would key to couplet 25 in Philip's (1955) key to *Chrysops* males. Not agreeing with either alternative, they would be separated by the first basal cell entirely infuscated and second basal cell mostly hyaline with at most an infuscated streak not reaching apex.

Ecology and Distribution: (April–September) This species usually was associated with the mixed bottomland hardwood forests of the rivers and streams throughout the state. It was also collected in the longleaf-slash pine and mixed pine-hardwood regions of the state.

Mature larva: This species could not be separated from *C. univittatus* in the short series examined. In general, the overall pubescent pattern of *upsilon* is darker; the posterior pubescence on the preanal segment more extensive, being somewhat wider on the lateral surfaces. (see also under *C. univittatus*)

Chrysops vittatus Wiedemann, 1821
(Fig. 80)

Length 6–10 mm; yellow; frontal callus yellow; abdomen with four black stripes; apical spot of wing extensive; apex of hyaline triangle just enveloping fork.

Variations: (Specimens examined—450) The specimens agree with Brennan's (1935) description and variations.

Ecology and Distribution: (April–October) A common pest species throughout much of its range (eastern North America), it was taken frequently throughout the state in all major vegetational regions except the prairie and coastal marsh. *C. vittatus* was reported widely distributed in the state (Hine, 1906, 1907a), and Jones and Bradley (1923, 1924) listed it as one of the five most annoying pest species of livestock in Louisiana.

Mature larva (Fig. 13): approximately 12 mm long, creamy white with extremely pale to light brownish pubescent markings.

Head capsule length: 1.4–1.5 mm.

Striations: Encircling all segments somewhat more closely spaced laterally.

Thorax: Anterior pubescent annuli extremely faint, covering aproximately ½, ⅓, and ¼, the length of the pro-, meso-, and metathorax, respectively. Short inconspicuous peg-like lateral projections present on the meso- and metathorax.

Abdominal segments 1–7: Anterior pubescence encircling segments 1–4, reduced laterally on 5, and absent laterally and reduced ventrolaterally on 6 and 7. Pseudopodial pubescent rings complete and joined with anterior pubescence dorsolaterally on segments 1–7 and ventrolaterally on 1–5. Posterior pubescence limited to a band encircling the preanal segment.

Anal segment: Posterior pubescent band encircling approximately ½ the segment, fading posteriorly; its anterior margin with a dorsolateral, anteriorly-directed, finger-like projection; ventrally the posterior pubescence encloses the anus. Anterior pubescence consists of several small scattered patches. A distinct oval-shaped pubescent spot is situated laterally in the anterior clear area.

Respiratory siphon: Long, 0.67–0.70 mm, approximately 3 times its basal diameter.

Comments: Two larvae were taken from mud in a water-filled ditch located in an upland hardwood forest of West Feliciana Parish. Another specimen was taken from the margin of the Amite River in East Baton Rouge Parish. Hine (1906) gives the life history for this species.

Subfamily Tabaninae

Genus Diachlorus Osten Sacken, 1876

Diachlorus ferrugatus (Fabr.) is the only known Nearctic member of the genus.

Diachlorus ferrugatus (Fabricius, 1805)

Length 7–10 mm; yellow; frons very narrow, about seven times higher than basal width; abdomen yellow-brown sublaterally with a broad median yellow stripe; wing with broad apical spot; legs yellow with fore tibiae black and swollen.

Variations: (Specimens examined—29) All agree with Stone's (1938) description.

Ecology and Distribution: (April–July) This species is a persistent feeder and readily attacks man. It was collected from marshes and swamps in the mixed bottomland hardwood forest regions. Except for a single collection in Winn Parish, it was taken in the southcentral and southeastern portions of the state. Jones and Bradley (1923) reported this species from East Baton Rouge and St. James parishes.

Genus Stenotabanus Lutz, 1913

Most Nearctic species of this genus are found in either coastal or desert environments. They are generally small, slender flies with bare to sparsely pilose eyes. Most species are grayish or pale in color and usually have a distinct stump vein basally at vein R_4. A bare basicosta and the absence of a dorsal excision on the third antennal segment are characteristic of the genus.

Stenotabanus magnicallus (Stone, 1935)

Length 11–14 mm, slender; grayish; frons broad, about 1⅓ times higher than basal width; eye with two median bands and a third at lower margin; basal callus protuberant; abdomen cream colored, darkened when discolored; wing hyaline, vein R_4 with stump.

Variations: (Specimens examined—22) Departures from Stone's (1938) description include the following: basal callus touching eyes; median callus variable, a slender line reaching vertex, or short and widened above, not reaching denuded area at top; small denuded spot at vertex not raised; shiny brown band between eyes at vertex absent. Male: upper facets of eye distinctly differentiated in size and color from lower facets; eye with two narrow bands beneath upper facets.

A small series of 20 males and 2 females collected from Santa Rosa County, Florida, exhibit some characters similar to those of *S. pechumani* Philip. One female has a thin median callus and both females have a small denuded patch at vertex. However, all males exhibit areas of large and small eye facets sharply differentiated as is typical of *S. magnicallus*—the area of upper facets is extensive and the eyes are not divided by a narrow midfrontal area.

Ecology and Distribution: (May–June) This species was collected by sweeping sea oats, *Uniola paniculata* L., along the sandy beaches of the Gulf of Mexico in Florida. It was reported from Grand Isle, Louisiana, by Drs. L. L. Pechuman and J. H. Roberts (personal communications).

Genus CHLOROTABANUS Lutz, 1909

Chlorotabanus crepuscularis (Bequaert) represents the single Nearctic species of this genus.

Chlorotabanus crepuscularis (Bequaert, 1926)

Length 13–16 mm; greenish yellow; basal and median calli absent; wing hyaline, costal cell yellowish; vein R_4 with a short stump.

Variations: (Specimens examined—49) All agree with Stone's (1938) description.

Ecology and Distribution: (May–August) This species was found throughout the state, primarily associated with lakes, streams, and bayous in the mixed bottomland hardwood forests. At times, it was locally abundant and was collected from late afternoon until approximately 11:00 p.m. It was not collected from the coastal marsh. Hine (1907a) and Jones and Bradley (1923, 1924) variously referred to this species as *Tabanus mexicanus* L. and *T. flavus* Macq.

Mature larva (Fig. 24): 22–29 mm long, body completely dark in appearance, clothed in black, brown, and golden mottled pubescence; preserved specimens brownish black in color; living larvae dark with greenish hues.

Head capsule length: 3.2–3.7 mm.

Striations: If present, obscured by pubescence.

Respiratory siphon: 0.75–0.84 mm long, approximately equal to its basal diameter.

Comments: Numerous larvae were collected from aquatic habitats in most of the vegetational regions of the state. This was one of the few species frequently collected swimming. It was locally abundant in heavily vegetated swamp ponds and borrow pits, and was generally absent from clear and/or moving waters. One specimen was collected biting the author's leg as he waded through a heavily vegetated swamp pond.

Jones and Bradley (1924) reared this species from larvae collected from a lake's surface and at the muddy margin of a brook. Wilson (1969) listed six species including *C. crepuscularis* as inhabiting forest soils. This is unusual in that the larvae of these species are usually confined to aquatic or margins of aquatic habitats.

Genus WHITNEYOMYIA Bequaert, 1933

Whitneyomyia beatifica (Whitney) represents the single Nearctic species of this genus.

Whitneyomyia beatifica atricorpus Philip, 1950

Length 13–16 mm; entirely dark brown to black; eye deep purple with four blue-green bands, the upper one parallel to frons near vertex; subcallus and upper genae denuded and swollen.

Variations: (Specimens examined—9) All agree with Stone's (1938) description for *W. beatifica* (Whitney) but lack white hair on the sides of abdominal tergites 1–4 as is present in that form. Philip (1950a) considered *atricorpus* as only a possible physiological melanistic variant when he gave it subspecific rank.

Ecology and Distribution: (April–June) The specimens were collected from mixed bottomland hardwood regions in Allen, Beauregard, Lafayette, Iberia, St. Landry, and Vermilion parishes; from a mixed pine-hardwood region of St. Helena Parish; and from a longleaf-slash pine forest in Tangipahoa Parish. Hine (1907a) referred to this species as *Tabanus lugubris* Macq.

Genus LEUCOTABANUS Lutz, 1913

This genus contains two Nearctic species and may be characterized by the following: denuded or sparsely pilose eyes; an ocellar tubercle; frons of female very narrow with long, slender median callus; third antennal segment with five divisions (four annuli); scutellum pallid.

Leucotabanus annulatus (Say, 1823)

Length 9–12 mm; gray to brownish; median callus a thin line and joined to basal callus; posterior margins of abdominal segments pale; wing hyaline; male, whitish.

Variations: (Specimens examined—62) All agree with Stone's (1938) description.

Ecology and Distribution: (May–September) This species was collected throughout the state except in the marsh region. Hine (1907a) and Jones and Bradley (1923, 1924) reported this species from Louisiana under the name of *Tabanus annulatus*.

Mature larva (Fig. 25): Rather small,

19–22 mm long; white with extremely faint to light golden-brown pubescent markings.

Head capsule length: 2.9–3.4 mm.

Striations: Distinct on all surfaces with rather uniform spacings.

Thorax: A narrow anterior pubescent annulus encircling each segment; paired lateral pubescent projections present on the prothorax extending approximately ⅓ the length of the segment.

Abdominal segments 1–7: Anterior pubescence narrowly encircling segments 1–3 or 4, incomplete on remaining segments becoming progressively reduced posteriorly. Pseudopodial pubescence complete except between pseudopods 2 and 3 on segments 2–5 and occasionally incomplete on segments 6–7. Posterior pubescence encircling segments 6–7, incomplete and often only faint or inconspicuous traces on segments 3–5.

Anal segment: Blunt and rounded; pubescence consists of a narrow posterior band, and the anal ring somewhat expanded laterally.

Respiratory siphon: 0.3–0.4 mm long, about ½ its basal diameter.

Comments: Numerous larvae were collected throughout the state with the exception of the marsh region. Especially productive were hardwood logs in advanced stages of decomposition. Occasionally, larvae were taken from forest floor litter and from tree holes. The holes ranged in depth from 8 to 40 cm. and were located from ground level to elevations of more than eight meters. Organisms most frequently noted in association with these larvae included millipedes, centipedes, mites, pseudoscorpions, isopods, annelids, snails, and numerous species of insects. Especially numerous were the larval forms of Mycetophilidae, Anthomyiidae, Scenopinidae, Limoniidae, Psychodidae, Muscidae, Stratiomyidae, and other Diptera. Other insects present were Collembola, elaterids, formicids, and lepidopterans.

Jones and Bradley (1923) collected larvae and pupae of this species from rotten logs and stated that with the exception of a single specimen of *Tabanus fulvulus*, no other species (tabanid) was reared from larvae found in such material.

The larvae of *L. annulatus* superficially resemble those of terrestrial *Tabanus molestus*. Both have distinct striations, somewhat reduced pubescent pattern, and a blunt rounded anal segment with the respiratory siphon about ½ as long as its basal diameter.

Genus TABANUS Linnaeus, 1758

This is the largest Nearctic genus of the Tabanidae and contains most of the economic pest species. Commonly known as horse flies, members of the genus vary considerably in size from small (8 mm) to over 30 mm, have bare to sparsely pilose eyes, and have a third antennal segment with five divisions (four annuli).

Tabanus aar Philip, 1941

Length 18–25 mm; reddish brown; eye purple with two green bands; frons at least 6.5 times higher than basal width; abdomen with a median row of small indistinct grayish triangles; wing faintly infuscated, darker along vein margins.

Ecology and Distribution: This species was not taken in Louisiana during the present study but was listed from the state by Philip (1950b). It was collected in northwest Florida and lower Mississippi in longleaf-slash pine forests. *Tabanus aar* is somewhat similar in appearance to *T. turbidus* Wied. and like *turbidus* it is commonly collected in late evening to well after dark. Both species were frequently taken in light traps.

Tabanus abdominalis Fabricius, 1805

Length 18–25 mm; orange to brown; eye purple with two green bands; frons at least five times higher than basal width; abdomen usually with a median row of dark spots on anterior of tergites; fore tibia bicolored; wing fuscous, furcation and cross veins margined with brown; cell R_5 closed.

Variations: (Specimens examined—11) Departures from Stone's (1938) description include the following: basal callus occasionally not touching eyes at base; occasionally scutellum concolorous with olive brown mesonotum, black when discolored.

Members of this species are highly variable, and some individuals resemble specimens of *T. sulcifrons* Macq. so closely that positive separation of the two species is difficult. The criteria used in separating this species from *T. sulcifrons* were given

by Pechuman (1954) and are as follows: narrow frons, closed first posterior cell (cell R_5), no evident abdominal triangles, and wholly black femora.

Ecology and Distribution: (June–August) This species was collected from the mixed bottomland hardwood forests of Calcasieu, DeSoto, East Baton Rouge, East Feliciana, Grant, Iberville, Lafayette, Tangipahoa, and Winn parishes. Hine (1907a) reported this species from Beauregard and Tensas parishes, and Jones and Bradley (1923, 1924) recorded the seasonal occurrence from June to October.

Tabanus acutus (Bigot, 1892)

Length 16–21 mm; pale brownish with a broad median light stripe on abdomen; eye green with three purple bands, frons 3.5–4 times higher than basal width; wing lightly fuscous with a spot at furcation.

Variations: (Specimens examined—60) Departures from Stone's (1938) description include the following: third antennal segment occasionally darkened toward the distal portion; middle and hind tarsi usually darkened.

Ecology and Distribution: (May–September) This species is active in daylight as well as after dark and is commonly collected at lights. Specimens were taken along the coastal marshes from Florida to Texas. Occasionally, a few individuals were collected inland from these areas. Hine (1907a) reported this species from Cameron and Plaquemines parishes.

Tabanus americanus Forster, 1771

Length 24–33 mm; dark with deep reddish hues; eye bright green; frons about four times higher than basal width; wing hyaline with infuscated costal cell; tufts of white pile about wing base.

Variations: (Specimens examined—65) Departures from Stone's (1938) description include the following: dorsal projection of third antennal segment varying from short and rounded to prominent, almost reaching the annulate portion. Genal and pleural hair occasionally white.

Ecology and Distribution: (April–August) This species was commonly collected throughout the state from all major vegetational regions except the prairie. Hine (1907a) also reported this species widely distributed in the state.

Mature larva (Fig. 38): large, 51–55 mm; completely clothed in grayish brown to dark brown pubescence, varying somewhat in intensity from darker dorsally to slightly lighter ventrally. Pubescence darkest on anal and preanal segments. Small pale spots present in a patterned arrangement on abdominal segments (approx. 20 per segment).

Head capsule length: 6.1–6.6 mm.

Striations: If present, obscured by pubescence.

Respiratory siphon: 1.9–2.2 mm, somewhat longer than its basal diameter.

Comments: The description is based on larval exuviae—in general living specimens are somewhat lighter in appearance. Four larvae were collected from mixed bottomland hardwood forest regions of St. Landry and Assumption parishes. The larvae were terrestrial in moist areas of the forest floor. These areas were occasionally flooded for a few days to several weeks during periods of heavy rains, especially during December, January, and May for the St. Landry location and during July, August, and September for the Assumption area; however, most of the year no standing water was present at the collecting sites. All specimens were removed from decaying logs. One specimen was taken from frass of passalid beetles in a partially-decomposed, water tupelo log. Other associated insects were mycetophilids, scenopinids, psychodids, and Collembola.

Jones and Bradley (1924) collected three larvae (reared) from the muddy margin of a shallow pool.

Tabanus aranti Hays, 1961

Length 15–22 mm; black; eye deep purple with two dark bronze bands; frons usually 4–5 times higher than basal width; wing dark.

Variations: (Specimens examined—28) Departures from Hays (1961) description include the following: occasionally height of frons greater than five times its basal width.

This species superficially resembles *T. atratus* Fabr. but is readily distinguished by its smaller size, narrower frons, and pollinose

genae. It is more closely related to *T. nigrescens* P. de B. and *T. colon* Thun. but may be separated by the characters listed in the key.

Ecology and Distribution: (May–June) This species was not commonly collected. One specimen was collected in Washington Parish, Louisiana. It was reared from a larva taken at the margin of a small stream in a longleaf-slash pine region. Two adults were taken in Tangipahoa Parish and others in Alabama.

Mature larva (Fig. 34): Rather large, 40–47 mm long; creamy white to light yellow with extremely pale to medium brown pubescent markings.

Head capsule length: 5.4–6.0 mm.

Striations: Present laterally on segments 1–10; absent or inconspicuous on dorsal and ventral aspects. Anal segment with conspicuous striations below the lateral pubescent arm and posterior to the anus. Anterior ⅓ of segment with very fine striations visible under high magnifications giving this area a shadowed appearance.

Thorax: Anterior pubescent annuli somewhat wider laterally. Lateral surface of prothorax with two pubescent arms tapering posteriorly and extending about ¾ the length of the segment. Meso- and metathorax with lateral pubescent projections, the middle pair extending approximately ¾ and ½ the length of their respective segments; the dorso- and ventrolateral projections extending approximately ½ and ⅓ the length of the meso- and metathorax, respectively. These projections may appear to traverse the entire length of the segment due to the presence of many fine striations and/or fine adherent debris.

Abdominal segments 1–7: Anterior pubescence encircling at least segments 1–4, becoming less conspicuous and somewhat reduced on remaining segments. Pseudopodial pubescent rings usually complete and connected with anterior pubescence ventrolaterally on segments 1–6. Posterior pubescence present on all segments ranging from inconspicuous colorless traces on anterior segments to a wide conspicuous band on the preanal segment.

Anal segment: Pubescence distinct, consisting of anal and posterior rings, the latter joined laterally with an anteriorly-directed, clubbed arm covering about ½ the length of the segment. Generally, three pubescent spots varying in size and intensity located somewhat dorsal to the arm.

Respiratory siphon: 1.5–1.7 mm long, less than 1.5 times its basal diameter and possessing a stigmatal spine.

Variations: Anterior and posterior pubescence in certain areas of the abdomen may be very faint and seen only as slight shadows, if at all. This may be especially true for the anterior pubescence in front of pseudopods 2, 3, 4, and posterior pubescence of the anterior abdominal segments. The lateral pubescent arm of the anal segment may be incomplete, not reaching the posterior pubescent ring. In some cases, the lateral arm may narrowly join the anal ring pubescence.

Comments: In addition to the Louisiana specimen, 38 larvae were collected from Lee County, Alabama. Most were taken from the margin of a shallow beaver pond situated in a hardwood forest. (See also Comments under *T. nigrescens*.)

Tabanus atratus Fabricius, 1775

Length 20–31 mm; black; eye dark with a narrow black median band and a wider black band below; frons 2–2.5 times higher than basal width; wing dark.

Variations: (Specimens examined—50) All agree with Stone's (1938) description.

Ecology and Distribution: (April–October) This species was found throughout the state from all major vegetational regions; however, it was collected most frequently in the mixed bottomland hardwood forests and seldom in the open pine woods. Hine (1906) gives the life history of this species and (1907a) lists *T. atratus* (in key *T. striatus*, lapsus) as state wide in occurrence.

Mature larva (Fig. 37): Large, 50–63 mm long; cream colored with conspicuous medium to dark brown pubescent markings on all segments.

Head capsule length: 6.3–7.3 mm.

Striations: Present laterally on segments 1–10 and occasionally ventrally behind the anus where they are faint and broken; absent elsewhere.

Thorax: Prothoracic annulus with a distinct lateral pubescent bib extending about ¾ the length of the segment. Meso- and metatho-

racic annuli with conspicuous lateral projections; usually one meso- and all metathoracic projections joined with posterior pubescent rings; two or three mesothoracic arms often merging into a solid mass and extending at least ¾ the length of the segment.

Abdominal segments 1–7: Anterior and pseudopodial pubescence joined broadly and connected with posterior pubescent rings by a dorsolateral pubescent bar on all segments; most segments with lateral and ventrolateral projections extending from the pseudopodial pubescence and directed toward corresponding projections from the posterior pubescent rings; these may form one or more continuous lateral bars on segments 1, 6, and 7. Middorsally, a pubescent projection extends posteriorly from the pseudopodial annulus ¼ to over ½ the length of the segments.

Anal segment: Pubescence extensive, covering segment with the exception of a dorsal to dorsolateral saddle-shaped clear area and ventral clear areas anterior and posterior to the anal lobes.

Respiratory siphon: Truncate apically, 1.7–2.3 mm long; about equal to its basal diameter.

Variations: In several specimens the middorsal pubescence extends the length of all abdominal segments and joins the posterior pubescence, forming a dark, wide dorsal band continuous on the anal segment where it isolates a small dorsolateral clear window on each side. In general, in these variants, the pubescence is much more extensive than on the normal body pattern, especially the lateral pubescence which may form two or more continuous bars on abdominal segments 1–7. This increase in the amount of pubescence may be the result of the larvae going through additional instars since early instar larvae exhibit less pubescence than older and more mature larvae.

Comments: Numerous larvae were found throughout the state in all major vegetational regions; however, they were collected most frequently from aquatic habitats on the floodplains of the larger rivers. Larvae were collected from the sandy beaches of fast-flowing streams, flood-control ditches, artificial impoundments, cattle water troughs, and marsh and swamp lakes. They were usually associated with the organic muck at the water's edge although some individuals were collected swimming near the surface.

Jones and Bradley (1923) collected and reared numerous larvae of this species. The larvae were maintained in moist sand in small glass jars and fed earthworms. Attempts to rear them on nutrient agar were unsuccessful.

Tabanus calens Linnaeus, 1758

Tabanus giganteus Degeer. Stone, 1938, USDA Misc. Publ. 305, p. 84.

Length 22–28 mm; brown with blackish abdomen; eye unicolorous; frons 4.5–5 times higher than basal width; antenna brownish orange; wing faintly infuscated.

Variations: (Specimens examined—6.) All agree with Stone's (1938) description.

Ecology and Distribution: (August) Specimens were taken from bottomland forests in Caddo, Claiborne, and St. Landry Parishes. Jones and Bradley (1923, 1924) referred to this species as *T. giganteus* and collected it July–October near Baton Rouge.

Tabanus cheliopterus Rondani, 1850

Length 15–21 mm; orange-brown; eye purple with two green bands; frons 2.5–3.5 times higher than basal width; abdomen with a median row of pale triangles; wing lightly fuscous with furcation and veins margined with brown.

Variations: This species is variable in certain characters. Lighter specimens (*T. cheliopterus cheliopterus*) usually have palpi, legs, and venter of abdomen light reddish brown. *Tabanus cheliopterus* var. *fronto* is a slightly larger, darker form with the above features brown to dark brown. In a small series (42 specimens) of *T. cheliopterus* (U.S. National Museum and the author's collection) there is intergradation in both leg and body coloration, and it may be that the varietal status for the darker form is unwarranted.

Ecology and Distribution: Hine (1907a) recorded this species under the name of *T. fronto* O.S. The description he gives (p. 48) could have included both light and dark forms. A single Louisiana specimen examined by the author (USNM) was a light colored male *T. cheliopterus* collected at New Orleans in August.

Tabanus coarctatus Stone, 1935

Length 14–18 mm; brownish; eye purple with two blue-green bands; frons 5–7 times higher than basal width; abdomen with a median row of pale triangles; wing nearly hyaline with a faint spot at furcation.

Variations: (Specimens examined—10) All specimens exhibit variation from Stone's (1938) description in the following characters: apical portion of fore tibiae and all tarsi fuscous; posterior bands of abdominal tergites not forming sublateral triangles. Two specimens have the scutellum with white hair. Certain specimens are similar to *T. equalis* Hine but can usually be separated by using the combination of characters given in the key.

Ecology and Distribution: (May–June) This species was collected from the longleaf-slash pine forests of Florida, Alabama, Mississippi, and Louisiana, and from an upland hardwood forest in West Feliciana Parish.

Tabanus colon Thunberg, 1827

Tabanus nigrescens var. *atripennis* Stone. Stone, 1938, USDA Misc. Publ. 305, p. 93.

Length 20–26 mm; dark brown to black; eye dark golden with three purple bands, the upper one fading; frons about 3.5–4.5 times higher than basal width; wing uniformly smoky with a spot at furcation.

Variations: (Specimens examined—9) Departures from Stone's (1938) description include the following: height of frons may be nearly 4.5 times its basal width; occasionally third antennal segment, except extreme apical tip, orange. Closely related to *T. nigrescens* P. de B., *T. colon* is separated by its uniformly infuscated wing.

Ecology and Distribution: (June–July) Seldom collected, this species was taken in the longleaf-slash pine forests of Florida and Mississippi, and five specimens were taken from longleaf pine forests in Washington and Tangipahoa parishes.

Tabanus cymatophorus Osten Sacken, 1876

Length 17–22 mm; gray and brown; eye purple with two green bands; frons about 4.5 times higher than basal width; abdomen with a median row of pale triangles and a sublateral row of pale oblique spots on each side; wing nearly hyaline, furcation and cross veins margined with brown.

Variations: (Specimens examined—11) All agree with Stone's (1938) description. Superficially resembling *T. reinwardti* Wied., *T. cymatophorus* is readily distinguished by its narrower frons.

Ecology and Distribution: (May–October) This species was associated primarily with the mixed bottomland hardwood forests in Acadia, Ascension, Calcasieu, East Baton Rouge, and Iberville parishes. Hine (1907a) recorded this species from Acadia Parish and stated that it was not known to be abundant. Jones and Bradley (1924) collected a larva (reared) from the edge of a shallow pool in East Baton Rouge Parish.

Tabanus eadsi Philip, 1962

Length 10–12 mm; yellowish and brown; eye green with one reddish purple band; frons about 3–3.5 times higher than basal width; abdomen with a middorsal pale stripe and two submedian brownish stripes; first three tergites yellowish laterally; wing hyaline, costal cell infuscated.

Variations: (Specimens examined—7) Departures from Philip's (1962) description include the following: frontal index varying from 1:2.8 to 1:3.4; basal callus narrowly joined to median callus; color of palpal hair varying from entirely yellow to mixed black and yellow; fore coxae concolorous with pleurae, occasionally with black hair; middle and hind femora and all tarsi, black; sides of first three abdominal tergites and venter of first three sternites, dull yellow-orange.

This species is very similar to *T. quinquevittatus* Wied., and geographic variation could account for observed differences. The males of *T. eadsi* cannot be consistently separated from those of *quinquevittatus*. The antennae, palpi, and extent of upper eye facets in a male *quinquevittatus* (Fairfield Co., Ohio) is nearly identical to that of a paratype (U.S. National Museum) of *eadsi* from Galveston, Texas. While it is possible that *eadsi* is only a subspecies of *quinquevittatus*, the restricted habitat and their early seasonal appearance give support for their distinctiveness.

Ecology and Distribution: (April–May) Four specimens were taken from the coastal marsh of Cameron Parish and two from the coast of Chambers Co., Texas. They were collected flying with *T. nigrovittatus* Macq.

Tabanus endymion Osten Sacken, 1878

Length 13–18 mm; brownish; eye purple with two blue-green bands; frons about four times higher than basal width; third antennal segment with no dorsal excision; abdomen with a median row of pale triangles; wing nearly hyaline, furcation and cross veins margined with brown.

Ecology and Distribution: (July–August) This species was collected from the longleaf-slash pine forests of northwest Florida but was not collected in Louisiana during the present study. It was reported from the state by Philip (1950b).

Tabanus equalis Hine, 1923

Length 16–25 mm; reddish brown; eye purple with two green bands; frons 4–5.5 times higher than basal width; third antennal segment dark brown to black; legs uniformly reddish brown; wing usually hyaline, veins in basal portion occasionally margined with brown, usually spot at furcation; abdomen with a median row of pale triangles.

Variations: This species is similar to *T. turbidus* Wied. but usually can be distinguished by the presence of a black third antennal segment, frons ratio less than 1:5.5, and wing veins not margined with brown. *Tabanus turbidus* usually exhibits an orange third antennal segment, frons ratio 1:6 or greater, and wing veins margined with brown. Some intermediate specimens from Louisiana have frons ratios as great as 1:6.5, but in other characters they are similar to *equalis*. Other intermediate specimens exhibit certain *turbidus* characters such as frons ratio 1:6 and light brown infuscation along wing vein margins; however, the third antennal segment is black. Most *equalis* specimens examined from Louisiana exhibit an entirely black third antennal segment; whereas, specimens from more northern areas (Kansas, Missouri and Iowa) usually exhibit a third antennal segment with black in the middle but brown on the apical and basal portions. Certain intermediate specimens are difficult to assign to either taxon. In a series of 873 specimens from 15 states from Florida to Iowa and Oklahoma to North Carolina (*turbidus* exhibits a southeastern distribution while *equalis* is somewhat more to the north and west), 98 intermediates were seen. Most of the intermediates came from Louisiana, Arkansas, and Tennessee.

A comparison of the variation in populations of *equalis* and *turbidus* indicates that these two forms could be members of the same species, each representing a geographically defined subspecies with some degree of overlap in certain areas. However, at this time it seems unwarranted to change the status of these two well known species to subspecific rank. Until conclusive information is available they are best treated as distinct species with, perhaps, a limited amount of hybridization occurring in regions of overlap.

Ecology and Distribution: (April–August) *Tabanus equalis* and *turbidus* were primarily associated with the mixed bottomland and upland hardwood forests throughout the state. They were collected frequently from late afternoon until after dark, and large numbers were taken using light traps. Jones and Bradley (1923, 1924) listed *T. turbidus*, *T. aequalis* (= *T. equalis*) and *T. uniformis* (= *T. equalis*) from the state.

Tabanus fairchildi Stone, 1938

Length 13–18 mm; grayish black; eye bronze green with one purple band; frons 3.5–4 times higher than basal width; antenna black; abdomen with a median row of pale triangles and a sublateral row of pale spots on each side; wing hyaline.

Variations: (Specimens examined—15) All specimens exhibit variation from Stone's (1938) description in the following characters: sublateral spots of abdomen touching hind margins of most tergites; median abdominal triangles varying from very slender to medium in width; triangle on second tergite not noticeably larger than others; mesial surface of fore femora dark brown to black.

A comparison of Louisiana adults with specimens provided by Dr. L. L. Pechuman (collected Ludlowville, N. Y.—near type locality) did not show any major variation although larvae from this location described by Teskey (1969) show variations from Louisiana specimens. Larvae from Tennessee and North Carolina described by Goodwin (1967), at least in some characters, appear to be closer to the La. specimens than the New York larvae.

Ecology and Distribution: (April–June)

T. fairchildi was taken near small streams that drain mixed pine-hardwood forests in East Feliciana and Natchitoches parishes. It was also taken from the longleaf-slash pine region of Tangipahoa and Washington parishes.

Mature larva (Fig. 39): Moderate in size, 30–36 mm long; cream colored with light to medium brown pubescent markings.

Head capsule length: 4.0–4.1 mm.

Striations: Present laterally and dorsally on segments 1–10 and ventrally on 4–10; incomplete or absent ventrally on thoracic segments. Anal segment with relatively wide striations dorsally and posterior to the anus; very fine and inconspicuous on anterior ⅓ of segment.

Thorax: Anterior pubescent annulus of prothorax with a lateral bib; meso- and metathoracic annuli with lateral projections extending approximately ¾ the length of the segments. Traces of posterior pubescence occasionally present laterally and middorsally on the metathorax.

Abdominal segments 1–7: All except dorsal pseudopods on segments 1–4 or 5 long and conspicuous with from 5 to 15 curved spines arranged in a semicircular pattern. Anterior pubescence encircling segments 1–2, incomplete and diminishing progressively on remaining segments. Pseudopodial pubescence encircling segments 1–2 or 3, continuous with anterior pubescence on segment one, and joined with anterior pubescence dorso- and ventrolaterally on two. Posterior pubescence present on all segments becoming progressively more conspicuous on posterior segments. A pubescent bar is present dorsolaterally on abdominal segment seven.

Anal segment: Pubescence distinct, consisting of anal and posterior rings, the latter expanded dorsally and extending an anterior projection occupying about ⅓ the length of the segment. Remaining pubescence consists of a lateral pubescent bar and one conspicuous and usually two smaller, less distinct pubescent spots dorsal to the bar. Immediately anterior to the anus, a ventral row of curved spines is situated on a protruding lip or anal pseudopod.

Respiratory siphon: 1.0–1.2 mm long, less than twice its basal diameter.

Variations: In some specimens the lateral arm of the anal segment appears to be joined to the median middorsal pubescent projection. An accumulation of adherent debris was present on several specimens being especially apparent on the anal segment.

Comments: Six larvae were taken beneath a layer of moss covering a partially submerged log in a beaver dam. Large numbers of aquatic insects were present in the dam which crossed a narrow, sandy-bottom stream. This stream was located in a mixed pine-hardwood forest in East Feliciana Parish. The above habitat is unusual in that the larvae of this species have been recorded only from beneath stones in riffle areas of streams (Stone, 1938; Roberts, 1962; Teskey, 1969).

Tabanus fulvulus Wiedemann, 1828

Length 12–16 mm; orange-yellow; eye green with three reddish purple bands; frons 5–7 times higher than basal width; palpi yellowish; pleurae and genae with yellow hair; abdomen with three rows of pale yellow spots, those of median row contiguous; wing subhyaline to hyaline with costal cell lightly infuscated.

Variations: 70 specimens were examined from Louisiana, Mississippi, Alabama, Florida, Tennessee, and North Carolina. Departures from Stone's (1938) description include the following: height of frons ranging from about 5.5 to 7 times its basal width; mesonotum dark golden; wing usually subhyaline; occasionally distal ½ of fore tibiae, extreme apices of middle and hind tibiae, dark; hind femora sometimes orange-brown with gray pollen.

Tabanus fulvulus closely resembles *T. pallidescens* Phil. (For additional information see discussion under latter species.)

Ecology and Distribution: (May–July) *T. fulvulus* was collected in the mixed pine-hardwood forests of East Feliciana, St. Helena, and Winn parishes. It was also taken from the upland hardwood forests of West Feliciana Parish and the longleaf-slash pine regions of Tangipahoa and Washington parishes.

Jones and Bradley (1923) recorded a larva of *T. fulvulus* (reared) from a rotten log; however, Pechuman (1962) stated that the *fulvulus* of Jones and Bradley was actually *T. pallidescens*, and the *fulvulus* recorded

by Hine (1907a) included, in part, *T. pallidescens* and *T. wilsoni* Pech.

Tabanus fuscicostatus Hine, 1906

Length 10–14 mm; brown; eye green with one reddish purple band; frons about 3.5–4 times higher than basal width; abdomen with a median pale stripe and a row of sublateral spots on each side; wing hyaline with distinctly infuscated costal cell.

Variations: (Specimens examined—130) Departures from Stone's (1938) description include the following: basal and median calli occasionally black; median callus variable, occasionally a small circular dot, or absent to very slim; thorax frequently olive-gray in appearance; apices of middle and hind tibiae usually darkened; femora usually dark brown to black; abdominal triangles occasionally widened on posterior margins; sublateral spots of tergites 2–4 sometimes reaching anterior and posterior margins, giving the abdomen a 3-striped appearance.

Forms of *T. fuscicostatus* from some areas exhibit the following characters either singly or in combination that are similar to those of *T. mularis* Stone: black basal calli, femora dark brown to black, and the lateral regions of the abdomen almost black. Certain of these specimens are difficult to assign; however, using the combination of characters given in the key, they can usually be separated.

Ecology and Distribution: (April–September) This species was found throughout the state usually associated with the bottomland hardwood forests on the floodplains of major rivers. Adults were taken from emergence cages located at the margins of small swamp pools and over the moist soils of riverbottom hardwood forests. While these areas were primarily terrestrial, they were periodically flooded by heavy rains.

Several larvae thought to be this species were taken from this habitat, but all died before emergence. Wilson (1969) reported taking *T. fuscicostatus* larvae from forest soils in St. Landry Parish.

The *T. fuscicostatus* recorded by Hine (1907a) and Jones and Bradley (1924) probably included, in part, *T. mularis*. Jones and Bradley listed *fuscicostatus* as one of the five most annoying pests of livestock in Louisiana.

Tabanus imitans Walker, 1848

Tabanus maculipennis var. *imitans* Walker. Philip, 1966, Ann. Entomol. Soc. Amer. 59: 520.

Length 20–30 mm; dark with reddish purple hues; eye in life dark with a narrow median black band and a broad black band at lower margin; frons 3–4 times higher than basal width; antenna orange to orange-brown, third segment with a prominent, forward projecting, dorsal process; wing hyaline, furcation and cross veins margined with brown, costal cell and wing base darkly infuscated.

Fairchild (1966) and Philip (1966) examined a specimen from the Berlin Museum thought to be the type of *T. maculipennis* Wied., 1828, and both concluded that it was conspecific with *T. imitans* var. *excessus* Stone, 1938. Since the name *T. maculipennis* has priority over *T. imitans* Walker, 1848, *T. imitans excessus* was placed in synonymy. The two varieties, *T. imitans imitans* Walk., 1848, and *T. imitans pechumani* Philip, 1960, were placed as subspecies of *T. maculipennis*.

However, the presence of a prominent dorsal projection of the third antennal segment, the presence of a single median black eye band and an extensive black band at lower margin, the usually long slender median callus, and the grayish lavender hues of the thoracic dorsum, make *T. imitans* distinct from *T. maculipennis*. Based on morphological characters as well as the geographic overlap of *T. maculipennis* and *T. imitans*, I consider *T. imitans* distinct from *T. maculipennis*.

The status of the form *pechumani* is uncertain to the author, but the presence of a prominent dorsal projection on the third antennal segment would indicate its closer relationship to *T. imitans*.

Variations: 126 specimens were examined from Louisiana, Mississippi, Alabama, Florida, and North Carolina. Departures from Stone's (1938) description include the following: eye coloration (see above); frons ratio of most specimens 1:3.5–1:4; median callus variable, rarely separated from basal callus and only occasionally somewhat widened; occasionally median callus reaching a denuded spot at vertex; second palpal segment occasionally strap-like; dorsum of

thorax with grayish purple hues; tufts of hair around wing base sometimes black; abdomen often lacking median row of triangles—this variation was frequently observed on the specimens 25–30 mm in length; eye (relaxed) of male with a wide median green band in the middle of small facets, a stripe of bright purple above, and the remainder with background color appearing as a dark dull reddish purple.

Ecology and Distribution: (May–July) Three specimens were taken in Washington Parish near small streams that drain the longleaf-slash pine forests. Jones and Bradley (1923) did not give descriptions for specimens they reared as *T. fuscopunctatus* Macq. and *T. imitans* Walk. It is possible that the *T. fuscopunctatus* was *T. imitans* and their *T. imitans* were *T. maculipennis.*

Tabanus lineola lineola Fabricius, 1794

Length 10–16 mm; brownish to dark gray-brown; eye purple with three green bands, the upper two joined at outer margin of eye; average frons about five times higher than basal width and widened above; abdomen with a median pale stripe and a row of sublateral contiguous spots on each side; wing hyaline.

Tabanus lineola is a member of a complex which includes *T. lineola hinellus* Phil., *T. similis* Macq. (= *T. lineola scutellaris* Walk.), *T. subsimilis* Bell., and additional forms. The *T. lineola* considered here is the dark inland form.

Variations: (Specimens examined—750) Departures from Stone's (1938) description include the following: height of frons 4.5 to over 7 times its basal width; occasionally basal callus light tan and palpi yellow-cream; sometimes hind femora light tan; median stripe occasionally widened on the posterior margins of abdominal tergites. Other variations would include intermediate conditions between the typical *T. lineola* and *T. lineola hinellus.*

Ecology and Distribution: (April–October) This species was found in all major vegetational regions but most often in the mixed bottomland hardwood forests. The subspecies *T. lineola hinellus* generally replaced typical *T. lineola* in the coastal marshes.

Hine (1906, 1907a) and Jones and Bradley (1924) listed this species as one of the most abundant and pestiferous in Louisiana. Wilson (1963) reported *T. lineola, T. vittiger schwardti* Phil. (= *T. subsimilis* Bell.), and *T. fuscicostatus* Hine constituted 90 percent of the tabanids taken using a horse in West Baton Rouge Parish.

Mature larva (Fig. 2): Small to moderate in size, 22–25 mm long; creamy beige to pinkish with light to medium brown pubescent markings.

Head capsule length: 2.8–3.4 mm.

Striations: Present laterally on segments 1–10; absent dorsally and ventrally on thoracic segments and ventrally on the first seven abdominal segments; faint, incomplete stria sometimes present dorsally on abdominal segments. Anal striations distinct, visible on all but the anterior ⅓ of the segment.

Thorax: Anterior pubescent annulus of prothorax with a lateral pubescent bib on each side, the lateral arms and central portion of which extend approximately ¾ and ½ the length of the segment, respectively; four lateral meso- and metathoracic arms extend from the anterior annuli at least ¾ and ½ the length of the respective segments. Mesothoracic arms somewhat swollen apically. A faint narrow band of posterior pubescence present on the metathorax.

Abdominal segments 1–7: Anterior pubescence encircling segments 1–5, absent laterally on 6–7. Pseudopodial pubescent connections complete and joined with anterior pubescence dorso- and ventrolaterally. Posterior pubescence present on all segments, becoming progressively more conspicuous and complete on posterior segments.

Anal segment: Pubescence distinct, consisting of posterior and anal rings, the latter extending a dorsal projection or arm which curves posteriorly on the midlateral surface tapering and not reaching the posterior pubescence. A large, irregular pubescent spot is located dorsal to, and often joins narrowly with, the pubescent arm. A small, inconspicuous spot is often present anterior and somewhat dorsal to the large spot.

Respiratory siphon: 0.8–1.1 mm long, about equal to its basal diameter.

Variations: Considerable variation of pu-

bescence on the anal segment was noted. Dorsolaterally, there may be 1–2 conspicuous pubescent spots and from 1–2 small spots none of which touch the lateral arm. In some individuals, there was more variation in the anal pubescent pattern from one side to the other as there was between different specimens. One adult identified as *T. lineola hinellus* was reared from a larva which exhibited an overall darker pubescent pattern. This larva also exhibited certain variations that were found in some of the other *T. lineola* larvae, notably on the anal segment where the large dorsolateral pubescent spot joined the pubescent arm.

Comments: Twelve larvae were collected from mixed bottomland hardwood regions of St. Landry and East Baton Rouge parishes and from the mixed pine-hardwood regions of Claiborne, Tangipahoa, Union, and Webster parishes. They were located in moist forest soils, intermittently flooded ditches, in partially submerged logs at the margins of standing bodies of water, and in other moist depressions.

Jones and Bradley (1924) collected 24 *T. lineola* larvae, most of which were taken at pond edges in open areas. Wilson (1969) reported taking the larvae of this species from forest soils in St. Landry Parish.

Tabanus lineola hinellus Philip, 1960

Length 12–16 mm; yellowish brown; eye pattern as in typical *lineola* although stripes somewhat broader; frons usually 4–4.5 times higher than basal width; abdomen with a median light stripe and a row of sublateral contiguous spots on each side; wing hyaline.

Variations: (Specimens examined—140) The specimens of this subspecies agree with Philip's (1960) description. Overall appearance is similar to that of typical *T. lineola* except that *T. lineola hinellus* is lighter in color and slightly larger. Intermediates between the two forms are occasionally found inland from the coastal marsh and usually cannot be placed with certainty into either taxon.

Ecology and Distribution: (April–September) This subspecies was collected from the coastal marsh, and occasionally a specimen was taken inland. One adult of *T. lineola hinellus* was reared from a larva collected in Tangipahoa Parish. This larva varied slightly in appearance from *T. lineola* larvae (see under *T. lineola* larval variations).

Hine (1907a) referring to this form as *T. quinquevittatus*, reported it was one of the three most common species on the Gulf Coast.

Tabanus longiusculus Hine, 1907

Length 10–13 mm; brown; eye green with two purple bands and a purple triangle above with its base on frons; frons 4–5 times higher than basal width; antenna orange with annulate portion black; abdomen with a median pale stripe widened posteriorly on each segment, and a sublateral row of pale spots on each side; wing nearly hyaline with costal cell infuscated.

Variations: Twelve Louisiana specimens agree with Stone's (1938) description.

Ecology and Distribution: (June) Two specimens were collected in a longleaf pine forest of Natchitoches Parish, and ten specimens were taken from a longleaf-slash pine forest in St. Tammany Parish. Jones and Bradley (1923) recorded this species from Mound (Madison Parish), Louisiana. Pechuman (1962) reported that a specimen collected by Bradley at Mound (determined as *T. longiusculus* by Aldrich) was actually *T. wilsoni* Pech.

Tabanus maculipennis Wiedemann, 1828

Tabanus imitans var. *excessus* Stone. Stone, 1938, USDA Misc. Publ. 305. p. 87.

Length 17–23 mm; dark with deep reddish purple hues; eye in relaxed specimens greenish purple with two narrow reddish purple bands; frons 3–3.5 times higher than basal width; third antennal segment lacking a forward projecting process; wing hyaline, furcation and cross veins distinctly margined with brown, costal cell and wing base heavily infuscated.

Variations: (Specimens examined—39) This species is similar to *T. imitans* Walk., and in addition to the key characters listed above, *T. maculipennis* usually exhibits the following: median callus spindle shaped, narrowly attached to basal callus; dorsum of thorax with deep reddish brown hues; spots on wing more extensive than in *T. imitans*; and eye (relaxed) of male with a narrow median green stripe in middle of small

facets, remainder with purplish cast. (See discussion under *T. imitans.*)

Ecology and Distribution: (May–July) This species was collected from the mixed bottomland hardwood forests of the Amite and Pearl rivers in Ascension, Livingston, and St. Tammany parishes, and from a longleaf-slash pine region in Washington Parish.

Mature larva (Fig. 32): Rather large, 43–47 mm long; green in life with light to medium brown pubescent markings.

Head capsule length: 5.0–5.6 mm.

Striations: Present laterally on segments 1–10; absent dorsally and ventrally on thorax; inconspicuous striations occasionally visible dorsally and ventrally on abdominal segments 1–7. Anal striations conspicuous below the lateral pubescent arm; absent or inconspicuous elsewhere.

Thorax: Anterior pubescent annuli with two lateral prothoracic and 4 meso- and metathoracic lateral pubescent projections on each side extending approximately ¾ the length of the segments. Posterior pubescence limited to metathorax, where it consists of narrow traces on all but the midlateral regions.

Abdominal segments 1–7: Anterior pubescence encircling segments 1–6 or 7, varied in intensity, becoming extremely faint and inconspicuous ventrolaterally on the last three segments. Pseudopodial pubescent connections complete, joined with anterior pubescence dorsolaterally on segments 1–3 or 4 and ventrolaterally on 1–6 or 7. At least faint traces of posterior pubescence on all segments, most distinct and widest on preanal segment.

Anal segment: Pubescence distinct, consisting of anal and posterior rings joined by a curved arm situated laterally on the segment; two or three isolated pubescent spots lie dorsolaterally. Anterior pubescence consists of an irregular dorsal band which extends a pair of posteriorly-directed finger-like projections; a faint anterior ventrolateral pubescent area connects with the base of the pubescent arm.

Respiratory siphon: 1.3–1.6 mm long, approximately equal to its basal diameter and possessing a stigmatal spine.

Comments: Twenty-two larvae were collected from a mixed bottomland hardwood region in St. Tammany Parish. They were located in muck along the margin of a cypress swamp. Several other specimens were taken along the marginal area of a stream in a longleaf-slash pine region of Washington Parish.

Tabanus melanocerus Wiedemann, 1828

Length 14–20 mm; brown to dark grayish; eye uniformly dark; frons usually 5–6.5 times higher than basal width; abdomen with a median row of pale triangles; fore tibia bicolored; wing hyaline to subhyaline.

Variations: For some time, the separation of this species from *T. petiolatus* Hine has been a source of confusion. The key characters most frequently used (relative development of the median abdominal triangle of tergite two, frons width to height ratio, the presence or absence of a petiolate condition of cell R_5) do not consistently separate some specimens. In general, the smaller specimens usually exhibit certain characteristics of *T. petiolatus* (frons ratio 1:7, petiolate cell R_5), while the slightly larger *T. melanocerus* usually have a frons ratio of 1:5 to 1:6 and cell R_5 open. Nevertheless, intergradation of characters was noted in a series of 255 specimens examined from Louisiana, Mississippi, Alabama, Georgia, Tennessee, Kentucky, and Florida, during the present study.

Teskey (1969) noted that the larvae of *T. melanocerus* could be distinguished from those of *T. petiolatus* primarily by the presence of lateral abdominal striations on the latter species. His *T. melanocerus* lacked such striations. The pupae that were reared from these larvae were also divisible into two concordant groups. Four pupae of one of these groups were secondarily distinguishable, and the adults reared from these were determined as *T. petiolatus*. However, the separation of the adults did not entirely agree with their immature stages, and Dr. Teskey mentioned the possibility of having to recognize three species, all of which are indistinguishable in one or more stages, recognize the presence of hybrids in the population, or to consider this group as a single polymorphic species.

The larvae of these two species reared during the present study exhibited consider-

able intergradation in the development of the lateral abdominal striations (see larval description). Some adults identified as typical *T. petiolatus* were reared from larvae that almost completely lacked lateral abdominal striations while some *T. melanocerus* had weak lateral striations present. Therefore, the two species could not be consistently separated in the larval stage. Intergradation of characters between both species was observed in the adults that were reared from these larvae.

Due to the occurrence of intermediates in both the adults and larvae of *T. melanocerus* and *T. petiolatus*, these nominal species are probably conspecific. However, until further supportive evidence is presented such as multiple rearings from a single egg mass, these well known species are treated as distinct.

Ecology and Distribution: (May–Sept.) *Tabanus melanocerus* was commonly collected throughout the state. It was most frequently taken from the hardwood forests associated with upland and lowland streams and lakes and was not collected from the coastal marsh. Hine's (1907a) Louisiana specimens were actually *T. petiolatus*.

Mature larva (Fig. 29): Moderate in size, 28–34 mm long; creamy white; pubescence scanty, extremely pale to light brown where present.

Head capsule length: 4.3–5.0 mm.

Striations: Usually present laterally on the thorax where they vary in different specimens from weak to fairly distinct. Striations may be completely absent on abdominal segments 1–7 or present on from several to all segments varying in different individuals from faint and inconspicuous to complete and distinct. Anal striations occasionally absent; generally present below lateral pubescent arm and to some degree above the arm.

Thorax: Pubescence consists of a light brown anterior prothoracic annulus and a faint anterior mesothoracic, lateral band on each side; lateral pubescent projections and metathoracic pubescence absent.

Abdominal segments 1–7: Anterior and posterior pubescence absent; pseudopodial pubescent connections incomplete on all segments.

Anal segment: Pubescence light to moderate in intensity, consisting of rather distinct anal and posterior rings. A pubescent arm located dorsal to and sometimes joined with the anal ridge extends to the midlateral portion of the segment where it curves toward and occasionally connects with the posterior pubescent ring. In specimens where the lateral arm pubescence does not connect with the posterior and/or anal rings, the impression of the complete arm is evident due to the presence of fine striations.

Respiratory siphon: 1.1–1.3 mm long, less than twice its basal diameter.

Comments: Fourteen larvae of *T. melanocerus-petiolatus* were collected from East and West Feliciana, Natchitoches, and St. James parishes. All but one specimen taken in St. James Parish were associated with small, sandy-bottom streams found in pine or upland hardwood forests. Those specimens collected in East Feliciana Parish were found in a beaver dam.

Jones and Bradley (1924) collected a larva (reared) in mud at the edge of a swift flowing stream (East Baton Rouge Parish).

Tabanus moderator Stone, 1938

Length 17–21 mm; dark brown; eye purple with two blue-green bands; frons at least seven times higher than basal width and widened above; scutellum white; abdomen with a median row of pale triangles; wing faintly fuscous, furcation and cross veins margined with pale brown.

Variations: (Specimens examined—9) Departures from Stone's (1938) description include the following: frons ratio 1:7 to 1:8.5. Rarely, certain specimens resembling *T. molestus* Say and with frons ratios approximately 1:6.5 could not be assigned with certainty to either taxon.

Ecology and Distribution: (May) This species, active in late afternoon until well after dark, was taken from mixed pine-hardwood forests in St. Helena Parish and from a longleaf-slash pine region in Tangipahoa Parish.

Tabanus molestus Say, 1823

Tabanus molestus Say, 1823, J. Acad. Nat. Sci. Philad. 3: 31, female. Stone, 1938, USDA Misc. Publ. 305. p. 97. Philip, 1947, Amer. Midland Natur. 37: 310.

Tabanus molestus mixis Philip, 1950, Ann. Entomol. Soc. Amer. 43: 241. (New Synonymy)

Length 14–22 mm; dark brown to black; eye dark with two blue-green to bronze bands; frons 4–6 times higher than basal width; scutellum white; abdomen with a median row of pale triangles, spot on tergite two reduced; wing lightly fuscous, furcation and cross veins faintly margined with brown.

Variations: In general the specimens agree with Stone's (1938) description and variations.

During the present investigation, 423 specimens from Louisiana, Mississippi, Alabama, Florida, and Kentucky, were studied. Numerous characters were examined including facial pollinosity color, antennal and palpal color, ventral and pleural hair color, infuscation of the wings, and shape of abdominal triangles, as well as overall appearance. While typical representatives of both forms are quite distinct, discordant variation and the intergradation of many characters were observed.

Both subspecies are collected together and are sympatric throughout much of their range. Since this does not conform to the usage of the term subspecies (geographically defined populations), the utilization of the subspecific category is unwarranted. Consideration of the two forms as distinct species is not supported by the available evidence. Based primarily on the above reasons, I consider both of these forms as a single taxon.

Ecology and Distribution: (April–August) This species was commonly taken throughout Louisiana in all regions except the prairie and coastal marsh. It is especially active in late afternoon and will continue its activity after dark. Hine (1906, 1907a) and Jones and Bradley (1924) listed this species as common in Louisiana during June.

Mature larva (Fig. 26): Moderate in size, 29–37 mm long; creamy yellow with rather pale pubescent markings.

Head capsule length: 3.8–3.9 mm.

Striations: Distinct, rather evenly spaced and completely encircling all segments; finer anterior to the pseudopods and on the anterior portion of the anal segment.

Thorax: Anterior pubescent annuli present; lateral surface of prothorax with two pubescent projections extending approximately ¾ the length of the segment. Only the most dorsal and ventral of the lateral meso- and metathoracic projections developed, extending about ¼ and ⅓ the length of the respective segments.

Abdominal segments 1–7: Narrow dorso- and ventrolateral bands of anterior peg-like, spiney pubescence on all segments, becoming progressively fainter and reduced on posterior segments. Pseudopodial pubescent connections incomplete, broken between the lateral and ventrolateral pseudopods (pseu. two and three) on all segments and pseudopods one and two on segments six and seven. Pseudopodial pubescence differing somewhat on segments 6–7 by the presence of isolated pubescent spots between pseudopods two and three. Posterior pubescence limited to a narrow band on the preanal segment. Three evenly spaced lateral lines present, often only faintly visible on segments 1–4.

Anal segment: Pubescence consisting of an anal ring with a small dorsal projection and a narrow posterior ring usually extending a short lateral, anteriorly-projected point. Anterior to the point is a small isolated patch of lateral pubescence.

Respiratory siphon: Short, 0.4–0.5 mm long, about ½ its basal diameter.

Comments: Nine specimens were collected from several locations in the upland hardwood and mixed pine-hardwood regions of East and West Feliciana parishes. The larvae were usually taken from beneath moss on the steep banks of small, sand-bottom streams. These streams were intermittently flowing especially during July, August, and December. The larvae are listed as primarily terrestrial since they were collected a meter or more above the high water mark on the banks of these streams.

A female of *T. molestus* was captured and held following a blood meal on a mule. She oviposited six days later on the nylon cover of her container. A second egg mass was obtained six days following a blood meal from the author's arm (and 11 days after oviposition of first egg mass). The larvae emerged 11 and 10 days, respectively from the two

egg masses. The egg mass is distinct from those of other *Tabanus* known to the author and is described as follows: mass approximately 8 × 5 mm, slightly pointed at each end, eggs deposited in a single upright tier (on the under surface of nylon hose). The mass contained approximately 250 creamy white (2.6 mm long) eggs that turned black in a few hours. However, the entire mass was covered with a clear mucous-like secretion which was draped across the eggs and hardened into a white coating much like frosting on a cake.

Tabanus mularis Stone, 1935

Length 10–12 mm; eye green with one reddish purple band; frons 3–4 times higher than basal width; mesonotum olive gray; abdomen dark with a median pale stripe and usually indications of a sub-lateral row of pale spots on each side; wing hyaline with costal cell distinctly infuscated.

Variations: (Specimens examined—50) Departures from Stone's (1938) description include the following: height of frons usually closer to three times its basal width; genae and clypeus below antennae not tinged with yellow; sublateral abdominal stripes occasionally extensive, similar to those found in darker forms of *T. nigrovittatus* Macq. Certain specimens of *T. mularis* are difficult to separate from *T. fuscicostatus* Hine (see discussion under latter species).

Ecology and Distribution: (May–September) This inland species of the *T. nigrovittatus-quinquevittatus* complex was taken primarily from the mixed bottomland hardwood forests associated with upland and lowland streams and waterways. It was less frequently collected from the mixed pine-hardwood, longleaf-slash pine, and prairie regions.

Tabanus nefarius Hine, 1907

Length 20–24 mm; brown; eye dark with two green bands; frons usually 5–6 times higher than basal width; abdomen with a median row of pale triangles; wing fuscous with furcation and cross veins distinctly margined with brown; cell R_5 nearly or completely closed apically.

Variations: (Specimens examined—13) Departures from Stone's (1938) description include the following: basal callus light tan to chestnut brown; usually subcallus and most of genae light tan: clypeus grayish; second palpal segment variable, occasionally very slender; one specimen with frontal index 1:6.6; most without light-colored posterior borders on abdominal tergites.

This species resembles *T. sulcifrons* Macq. but can usually be separated by characters given in the key.

Ecology and Distribution: (June–August) Specimens were taken primarily from the mixed bottomland hardwood forests on the lower extremity of the Mississippi floodplain. They were collected in Iberia, Iberville, Jefferson, Lafourche, Livingston, and St. Tammany parishes. Hine's (1907b) original description of *T. nefarius* was based on three females, one taken near New Orleans and two taken at LeCompte, Louisiana. Jones and Bradley (1924) reported this species from St. John the Baptist Parish.

Tabanus nigrescens Palisot de Beauvois, 1809

Length 20–24 mm; dark brown to black; eye dark with three purple bands, the upper one fading; frons 3.5–4.5 times higher than basal width; wing fuscous, paler posteriorly, furcation and cross veins margined with brown.

Variations: (Specimens examined—3) Departures from Stone's (1938) description include the following: annulate portion of third antennal segment about ½ the length of basal portion.

Ecology and Distribution: (June–July) Collection of this species from the state was not confirmed during the present study (see under larval comments) although Louisiana would fall within the distribution listed by Philip (1965). Adults were collected from Mississippi and Alabama.

Mature larva (Fig. 33): Large, 50–55 mm long; creamy white with light to medium brown pubescent markings.

Head capsule length: 6.1–6.7 mm.

Striations: Present laterally on segments 1–10; absent on dorsal and ventral aspects; anal striations distinct below lateral pubescent arm, inconspicuous elsewhere. Anterior ⅓ of anal segment with extremely fine striations (visible under high magnifications) giving this area a shadowed appearance.

Thorax: Anterior pubescent annuli somewhat wider laterally; prothorax laterally with two pubescent arms extending over ½ the length of the segment. Meso- and metathorax with four lateral pubescent projections, the middle pair extending about ¾ and ½ the length of their respective segments; the dorso- and ventrolateral projections extending approximately ½ and ⅓ the length of the meso- and metathorax, respectively. These projections may appear to traverse the entire length of the segment due to the presence of many fine striations and/or presence of fine adherent debris.

Abdominal segments 1–7: Anterior pubescence varying in intensity, encircling segments 1–3 or 4; incomplete and becoming progressively reduced on remaining segments. Pseudopodial pubescent rings complete on segments 1–5 or 6, and joined with anterior pubescence ventrolaterally on at least 1–5. Posterior pubescence consists of a wide distinct band encircling the preanal segment and faint inconspicuous traces dorso- and ventrolaterally at least on segments 4–6.

Anal segment: Pubescence distinct, consisting of anal and posterior rings and a curved arm extending dorsally from the anal ring where it bends in the midlateral portion of the segment and reaches the posterior pubescent ring. One distinct, and 1–2 faint pubescent spots situated dorsolaterally above the arm.

Respiratory siphon: 1.5–1.7 mm, slightly longer than its basal diameter and possessing a stigmatal spine.

Comments: Two larvae were collected from the margin of a beaver pond in Lee County, Alabama. These resembled eight specimens collected from a small ditch in a similar habitat of upland hardwood forest in West Feliciana Parish, Louisiana. However, none of the latter was reared, and positive identification could not be made.

The larvae of *T. nigrescens* are very close to those of *T. aranti* Hays, the latter species having the prothoracic arms slightly wider with a more diffuse appearance, and the lateral pubescent arm of the anal segment usually not connected to the anal ring. Specimens of *T. aranti* are smaller in total body length and have a shorter head capsule.

Tabanus nigripes Wiedemann, 1821

Tabanus coffeatus Macquart. Stone, 1938, USDA Misc. Publ. 305. p. 100.

Length 11–16 mm; grayish black; eye uniformly dark; frons 4.5–5 times higher than basal width; subcallus usually partially denuded; abdomen with a median row of whitish triangles; posterior margins of tergites pale; wing hyaline.

Variations: (Specimens examined—83) All agree with Stone's (1938) description.

Ecology and Distribution: (April–September) *T. nigripes* was found primarily in the mixed bottomland hardwood forests of the Mississippi floodplain. It was also collected from hardwood forests associated with streams in Rapides, St. Tammany, Washington, and Winn parishes. Hine (1907a) referring to this species as *T. coffeatus*, indicated that it was not commonly collected.

Mature larva (Fig. 27): Small to moderate, 25–28 mm long; whitish with few pubescent markings.

Head capsule length: 4.0–4.6 mm.

Striations: Inconspicuous or absent; when present, usually faint or broken and visible only on lateral aspects of thorax and one or more abdominal segments.

Thorax: Prothoracic annular ring with a ventrolateral projection and usually a faint sparsely pubescent dorsolateral projection on each side, all extending approximately ¾ the length of the segment. Narrow inconspicuous anterior pubescent bands present laterally on the meso- and metathorax, the former with indications of short, peg-like lateral projections.

Abdominal segments 1–7: Anterior pubescence present only as faint traces midventrally on segments 1–2; pseudopodial connective pubescence incomplete, and posterior pubescence absent on all segments.

Anal segment: Pubescence moderate in intensity, limited to anal and posterior rings.

Respiratory siphon: 1.3–1.4 mm long, almost twice its basal diameter.

Comments: The larval description is based on four specimens collected in Lee County, Alabama. These were found at the margin of a small pond in a mixed pine-hardwood region.

Tabanus nigrovittatus Macquart, 1847

Length 9–16 mm; eye green with one reddish purple band; frons 3–4.5 times higher than basal width; mesonotum grayish to yellow; abdomen yellowish sublaterally with a pale median stripe; wing hyaline, costal cell lightly infuscated.

Variations: (Specimens examined—200) Departures from Stone's (1938) description include the following: rarely, palpi yellowish; basal callus occasionally with brown shades, and may be connected to median callus; costal cell hyaline to faintly infuscated. Color patterns range from dull and inconspicuous to bright and distinct.

The coastal marsh specimens of *T. nigrovittatus* are larger and lighter, while the occasional inland specimens are usually darker and exhibit intergradation in appearance with *T. mularis* Stone. Frequently, demes are recognized by the overall similarity of the specimens collected. A series from the Chandeleur Islands tend to be dull in overall body coloration with yellowish palpi and costal cells nearly hyaline.

Many specimens collected during this study exhibit some characters listed by Philip (1957) for *T. nigrovittatus fulvilineis*. However, these characters vary and intergrade with those of typical *T. nigrovittatus*. Some variations from Philip's description include attached median callus to a tridentate upper margin of the basal callus, and number and presence of indentations of this upper margin varying from none to several. Many specimens have the typical *T. nigrovittatus* abdominal pattern but have the apical ½ of the fore, and extreme apices of the middle and hind tibiae black, as well as the dark femora listed by Philip for some paratypes of *T. nigrovittatus fulvilineis*. It is doubtful that specimens of the latter form are anything more than occasional variants of typical *T. nigrovittatus*. However, at the present time insufficient material is available to confirm this hypothesis.

Ecology and Distribution: (April–October) This species was common on the coastal marshes, and at times extremely numerous. Occasionally, specimens were collected inland.

Hine's (1907a) description of *T. nigrovittatus* was based on one atypical specimen and is insufficient to determine what he had before him. The *T. costalis* Wied. of Hine (1907a), reported as abundant in coastal regions, was probably *T. nigrovittatus*. The *T. costalis* reported by Jones and Bradley (1924), lacking description, cannot be assigned with certainty to a known taxon.

Tabanus pallidescens Philip, 1936

Length 12–16 mm; orange-yellow; eye green with 1–3 reddish purple bands; frons about 5.5–7 times higher than basal width; palpi creamy white; pleurae and genae with white hair; abdomen with three rows of pale yellow spots, those of median row contiguous; wing hyaline to subhyaline with costal cell lightly infuscated.

Variations: Philip (1936) named *pallidescens* as a subspecies of *T. fulvulus* Wied. Variations from his description include the following: height of frons ranging from about 5.5 to 7 times its basal width; callosity light brown to black; occasionally distal ½ of fore tibiae, extreme distal portions of middle and hind tibiae, dark; middle and hind tarsi darkened.

Pechuman (1962) separated *T. pallidescens* from *T. fulvulus* at the specific level utilizing characters listed by Philip (1936), as well as some additional ones. Later Pechuman (personal correspondence) gave three characters which he found to be fairly consistent in separating *T. pallidescens* from *T. fulvulus*, and also mentioned that he had observed some intergradation in the antennal color and eye banding. The three characters which he listed for *T. pallidescens* are pale hind femora, pale coxae, and whitish palpi.

Approximately 950 specimens of *T. pallidescens* taken during the present study exhibit variations in the number of eye bands from 1 to 3, or absent, and the color of the apical portion of the third antennal segment from orange-yellow to black. In general, specimens with the darker antennae have the greater number of eye bands. The best distinguishing characters found to separate this species from *T. fulvulus* were the creamy white palpi, and the white hairs of the genae and pleurae. Utilizing these characters as criteria for separating *T. pallidescens* from *T. fulvulus*, only 39 specimens of the latter species were collected in Louisiana, and *T. fulvulus* was usually collected with *T. pallidescens*. In addition, there is an in-

tergradation of most characters and an overall similarity in appearance of the two species. This information would indicate the possibility that these are members of a single taxon exhibiting varying phenotypic expressions. However, the author is reluctant to synonymize these two well-known entities, and until larval information or genetic data are available to indicate otherwise, they are treated as distinct species.

Ecology and Distribution: (April–July) *T. pallidescens* was commonly collected throughout most of the state.

Tabanus petiolatus Hine, 1917

Length 13–17 mm; brown to dark grayish; eye uniformly dark; frons usually 6–7.5 times higher than basal width; abdomen with a median row of pale triangles; fore tibia bicolored; wing hyaline to subhyaline.

Variations: (See discussion under *T. melanocerus* Wied.)

Ecology and Distribution: (May–Sept.) This species was widely distributed throughout the state but was collected primarily in the mixed bottomland hardwood forests associated with the lower portion of the Mississippi floodplain.

Mature larva: (See description under *T. melanocerus*.)

Tabanus proximus Walker, 1848

Length 19–29 mm; brownish black with deep purple hues; eye purple with two green bands; frons 6–7 times higher than basal width; antenna orange; wing smoky with furcation and cross veins margined with brown; cell R_5 narrowed or closed apically.

Variations: (Specimens examined—40) All agree with Stone's (1938) description.

Ecology and Distribution: (June–September) This species was collected from the mixed bottomland hardwood forests associated primarily with the floodplains of major rivers. Hine (1906, 1907a) and Jones and Bradley (1923; 1924) reported this species from the state under the name of *T. benedictus* Whitney.

Mature larva (Fig. 35): Rather large, 48–54 mm long; creamy white with light to medium brown pubescent markings.

Head capsule length: 5.3–5.9 mm.

Striations: Present laterally on segments 1–10; wider, less conspicuous, and often broken dorsally and ventrally on the first seven abdominal segments; absent dorsally and ventrally on thoracic segments. Anal striations conspicuous below the lateral pubescent arm; usually weak and broken above; absent elsewhere on the segment.

Thorax: Anterior pubescent annuli somewhat broader laterally; lateral surface of prothorax with a pubescent bib, the lateral arms and central portion of which extend approximately ¾ and ½, respectively, the length of the segment; meso- and metathorax with thin lateral pubescent projections extending about ⅔ and ½ the length of the segments, respectively.

Abdominal segments 1–7: Pale anterior pubescence encircling segments 1–4 or 5; incomplete and progressively reduced on remaining segments. Pseudopodial pubescent rings complete on all segments, connected with anterior pubescence dorsolaterally on segments 1–2 or 4 and ventrolaterally on 1–5. Posterior pubescence present on segments 4–7, most conspicuous on preanal segment; scant traces may be present on segments 1–3 where they are extremely faint and inconspicuous.

Anal segment: Pubescence distinct, consisting of anal and posterior rings, the latter joined with a lateral clubbed arm extending approximately ½ the length of the segment. Two conspicuous irregular pubescent spots, and a small faint spot lie dorsolaterally above the arm; paired dorsal finger-like projections extend posteriorly a short distance from the anterior margin.

Respiratory siphon: 1.4–1.6 mm long, about equal to its basal diameter and possessing a stigmatal spine.

Variations: Occasionally the pubescent arm of the anal segment may be narrowly joined to the anal ring, and the two conspicuous dorsolateral pubescent spots sometimes join together.

Comments: Numerous larvae were collected from the mixed bottomland hardwood regions throughout Louisiana. They were found most often terrestrially in the moist floodplain soils of large rivers. Occasionally these areas were flooded during periods of heavy rains; however, most of the year no standing water was present.

Jones and Bradley (1924) reared two larvae of this species taken from the muddy margin of a slough in East Baton Rouge Parish.

Tabanus pumilus Macquart, 1838

Length 9–11 mm; dark brown to blackish; eye purple with two blue-green bands; frons 4.5–6 times higher than basal width; palpi creamy white with black hair; abdomen with three rows of pale spots; wing hyaline.

Variations: (Specimens examined—167) All agree with Stone's (1938) description. This small species superficially resembles *T. sparus* Whit. but can readily be separated by characters given in the key.

Ecology and Distribution: (April–July) This species was collected throughout the state. It was associated primarily with the bottomland hardwood and the mixed pine-hardwood regions. Hine (1906, 1907a) and Jones and Bradley (1923, 1924) recorded *T. pumilus* as a common early season pest of livestock in Louisiana.

Mature larva (Fig. 40): Rather small, approximately 18 mm long, creamy white with pale to medium brown pubescent markings.

Head capsule length: No measurement made.

Striations: Encircling all segments, slightly more closely spaced laterally; prothoracic striations inconspicuous and broken dorsally and ventrally.

Thorax: Anterior pubescent annulus of prothorax with two lateral projections on each side extending less than ½ the length of the segment; meso- and metathoracic annuli narrow, each with short pointed dorso- and ventrolateral projections.

Abdominal segments 1–7: Anterior pubescence encircling segments 1–4; incomplete and becoming progressively reduced on 5–7. Pseudopodial pubescent rings complete on segments 1–5; narrowly connected between pseudopods 2 and 3; joined with anterior pubescence dorsolaterally on segments 2–6 and ventrolaterally on 1–4. Posterior pubescence encircling segments 5–7, faint on 5; extremely pale, inconspicuous traces present on 3 and 4.

Anal segment: Pubescence consisting of an anal ring, two lateral posteriorly-pointed projections, a small isolated dorsolateral pubescent spot, and a dorsal median posterior strip.

Respiratory siphon: Long and slender, 1.1 mm long, over three times its basal diameter.

Comments: The description is based on one larva collected from the margin of a small, water-filled ditch in an upland hardwood forest of West Feliciana Parish.

Tabanus quaesitus Stone, 1938

Length 10–14 mm; brown; eye sparsely pilose with a single purple band; frons about 2.5–3.5 times higher than basal width; abdomen with three rows of pale spots, the median row slender; wing hyaline.

Variations: (Specimens examined—38) Departures from Stone's (1938) description include the following: frons noticeably narrowed above in some specimens; extent of median denuded area variable, occasionally entire vertex pollinose; basal callus light brown to black, variable in shape from transverse to nearly quadrate and rounded above; median callus variable, occasionally reduced to a small isolated spot; occasionally entire plate of third antennal segment orange; basicosta with sparse hair, sometimes almost completely bare; median triangles of abdomen occasionally absent posterior to segment two; abdominal venter entirely gray.

This species resembles *T. exilipalpis* Stone, the latter having been reported from Mississippi, Alabama, and other southeastern states. They are separated by characters listed in the key.

Ecology and Distribution: (April–June) This species was taken primarily from the mixed pine-hardwood forests of the mid-central and northern portions of the state.

Tabanus quinquevittatus Wiedemann, 1821

Length 10–13 mm; yellow-brown; eye green with one reddish purple stripe; frons about 3.5–4 times higher than basal width; thorax dull golden; abdomen brown with a median yellowish stripe and a sublateral stripe or row of spots on each side; wing hyaline, costal cell infuscated.

This species was not collected in Louisiana during the present study; however, since it is reported throughout much of central and eastern North America including Arkansas and Mississippi (Thompson and Pechu-

man, 1970), it should occur in Louisiana. The Louisiana record of *T. quinquevittatus* by Hine (1906, 1907a) was actually based on specimens of *T. lineola hinellus* Phil.

Tabanus reinwardti Wiedemann, 1828

Length 15–20 mm; dark gray; eye purple with two blue-green bands; frons about 2.5–3 times higher than basal width; abdomen with a median row of pale triangles and a row of sublateral pale spots on each side; wing hyaline, furcation and cross veins margined with brown.

Variations: (Specimens examined—3) Departures from Stone's (1938) description include the following: general color gray; denuded area at vertex absent; thoracic pleura and sternum gray pollinose with white hair; abdomen above gray to fuscous with a median row of broad white triangles which may be confluent with the sublateral spots along hind margin of each segment. Male: hair of genae white.

This species superficially resembles *T. cymatophorus* O.S. but can be distinguished by its wider frons.

Ecology and Distribution: (May) One adult was collected in a longleaf-slash pine forest of Tangipahoa Parish. Two other specimens (reared) were taken in the mixed pine-hardwood region of West Feliciana Parish.

Mature larva (Fig. 31): Moderate in size, 33–35 mm long; creamy tan with rather distinct pubescent markings.

Head capsule length: 4.5–4.6 mm.

Striations: Present laterally on segments 1–10; absent elsewhere on these segments except dorsally on 4–10 where they are faint and incomplete, most conspicuous on segment 10. Striations completely encircling anal segment.

Thorax: Anterior pubescent annuli broader laterally. Lateral surface of prothorax with a pubescent bib, the central portion and lateral arms of which extend over ½ and ¾, respectively, the length of the segment. Meso- and metathorax with lateral projections extending about ¾ and ⅔ the length of the segments, respectively. A narrow posterior pubescent band encircles the metathorax.

Abdominal segments 1–7: Anterior pubescence encircling segments 1–5; reduced laterally on 6 and laterally and ventrolaterally on 7. Pseudopodial pubescent rings complete on all segments and joined with anterior pubescence dorso- and ventrolaterally. Posterior pubescent bands encircling all segments, most distinct on the preanal segment.

Anal segment: Pubescence distinct, consisting of anal and posterior rings joined by a curved arm situated laterally on the segment. Three isolated pubescent spots lie dorsolaterally above the arm.

Respiratory siphon: 1.0–1.2 mm long, almost 1⅓ times its basal diameter.

Comments: Two larvae were collected from the marginal area of a stream in the mixed pine-hardwood region of West Feliciana Parish. Jones and Bradley (1923) collected a larva from the sandy margin of a sluggish brook near Baton Rouge.

Tabanus rufofrater Walker, 1850

Length 15–22 mm; reddish brown; eye in life brownish black with two light bronze bands; frons about 5–5.5 times higher than basal width; fore tibia unicolorous; abdomen with a median row of faint triangles; wing hyaline.

Variations: (Specimens examined—10) All specimens differ from Stone's (1938) description in the following character: hind femora with white hair and scattered black hairs on side and top.

Ecology and Distribution: (May) Four specimens were collected from the longleaf-slash pine regions in Tangipahoa and St. Tammany parishes. Specimens were also collected from the coastal longleaf-slash pine forests of Mississippi, Alabama, and Florida.

Tabanus sagax Osten Sacken, 1876

Length 12–17 mm; brownish; eye green with three purple bands; frons about three times higher than basal width; abdomen with a median pale stripe widened posteriorly on each segment, and a sublateral row of pale spots on each side; wing hyaline with costal cell infuscated.

This species was reported from Caddo and DeSoto parishes (Hine, 1906, 1907a). One Louisiana specimen in the U.S. National Museum labeled *T. sagax* (determined by Hine) was examined by the author and found to be *T. zythicolor* Phil.

Tabanus sparus milleri Whitney, 1914

Length 7.5–11 mm; grayish black; eye green with one purple band; frons about 5–5.5 times higher than basal width, abdomen with three rows of pale spots; wing hyaline.

Variations: (Specimens examined—44) Other than minor coloration differences and the occasional absence of the median abdominal triangles, the specimens agree with Stone's (1938) description. A few specimens did not reveal the single eye band when placed in the relaxing chamber, but when these individuals were submerged in water for several hours, a faint eye band could be observed. The author has not seen living specimens of typical *T. sparus* which are characterized by the absence of the purple eye band.

This species superficially resembles *T. pumilus* Macq. but can be distinguished by characters listed in the key.

Ecology and Distribution: (May–August) *T. sparus milleri* was collected primarily in the mixed pine-hardwood forests of East Baton Rouge, East Feliciana, Natchitoches, Rapides, St. Helena, and Winn parishes. It was also taken in the upland hardwood forests of West Feliciana Parish and the longleaf-slash pine region of Washington Parish.

Tabanus stygius Say, 1823

Length 19–25 mm; eye dark green with three purple bands, the upper one reduced; frons 3.5–4.5 times higher than basal width; thorax gray; abdomen black; wing smoky with furcation and cross veins margined with brown.

Variations: (Specimens examined—42) Departures from Stone's (1938) description include the following: median callus ranging from narrow to rather broad; basal callus reddish brown to black; annulate portion of antenna occasionally black.

Ecology and Distribution: (May–August) This species was taken primarily from the mixed bottomland hardwood forests in the southern part of the state. Jones and Bradley (1923, 1924) collected this species from New Orleans and Baton Rouge.

Mature larva (Fig. 36): Rather large, 48–52 mm long; creamy yellow with distinct brown pubescent markings on all segments.

Head capsule length: 5.2–5.3 mm.

Striations: Present laterally on segments 1–10; absent, or inconspicuous and broken on dorsal and ventral aspects. Striations of anal segment conspicuous, visible ventrally and ventrolaterally behind the anus.

Thorax: Anterior pubescent annuli distinct and somewhat widened laterally; lateral surface of prothorax with a pubescent bib; meso- and metathoracic segments with lateral projections extending about ¾ the length of the segments; mesothoracic projections somewhat swollen apically; a narrow band of posterior pubescence present on the metathorax and small patches present on the mesothorax.

Abdominal segments 1–7: Anterior pubescence distinct, encircling segments 1–6; incomplete ventrally on 7. Pseudopodial pubescent rings complete, joined with anterior pubescence dorso- and ventrolaterally on all segments. Posterior pubescent rings present, becoming progressively more conspicuous posteriorly from segments 1–7. Preanal segment with dorso- and ventrolateral pubescent bars connecting pseudopodial with posterior pubescence; incomplete pubescent lines present between the bars and incomplete lines present dorso- and ventrolaterally on segment six.

Anal segment: Pubescence distinct, consisting of anal and posterior rings joined laterally by a curved pubescent arm. Occasionally, a narrow band of anterior pubescence is present on the dorsal ½ of the segment. A large, irregular pubescent spot, and from one to two smaller spots are found dorsolaterally above the curve of the arm, and one laterally in front of the arm.

Respiratory siphon: 1.7–1.8 mm, slightly longer than its basal diameter and possessing a stigmatal spine.

Comments: Five larvae were collected from East Baton Rouge, Lafourche, St. Landry, and Vermilion parishes. Two specimens were taken from the margin of a ditch filled with water-hyacinth, *Eichhornia crassipes* (Mart.) Solms, in the coastal marsh region, and three were found at the margins of ponds in the mixed bottomland hardwood region.

Tabanus sublongus Stone, 1938

Length 11–15 mm; orange-brown; eye green with three purple bands; frons 3.5–4.5 times higher than basal width; abdomen with three rows of pale spots, the median row contiguous; wing nearly hyaline, costal cell faintly tinted with orange.

Variations: (Specimens examined—2) Departures from Stone's (1938) description include annulate portion of third antennal segment in one specimen brown (second specimen with antennae missing); mesonotum dark in both with sparse golden hair and yellowish pollen.

Ecology and Distribution: (June) Two specimens were collected from a longleaf pine region in Natchitoches Parish. Another specimen labeled Logansport (DeSoto Parish) is in the collection of Dr. C. B. Philip.

Tabanus subsimilis Bellardi, 1859

Tabanus vittiger schwardti Philip, 1942, Psyche, 14: 29–32.

Tabanus schwardti schwardti Philip. Philip in A. Stone et al., 1965, Agr. Handbook 276. p. 336.

Length 10–16 mm; brownish; eye purple with three green bands, the upper two joined at outer margin of eye; frons about 3.5–4.5 times higher than basal width; posterior portion of scutellum reddish; abdomen with a median pale stripe and a row of sublateral contiguous pale spots on each side; wing hyaline.

Variations: (Specimens examined—100) Departures from Philip's (1942) description include the following: frontal index less than 1:4.8; posterior ½ of scutellum occasionally with only a tinge of red; distal ¾ of hind femora in males occasionally reddish gray, and entire middle femora reddish tan; abdominal lines varying from light tan to blackish.

In overall appearance, this species is very similar to *T. lineola* Fabr., and is separated by characters given in the key. Generally, both species have similar geographic and seasonal distributions.

Ecology and Distribution: (March–October) This species was collected throughout the state but most often from the mixed bottomland hardwood forests.

Tabanus sulcifrons Macquart, 1855

Length 14–24 mm; brownish to orange-brown; eye purple with two green bands; frons 4–5.5 times higher than basal width; fore tibia often bicolored or paler basally; abdomen with a median row of pale triangles; wing lightly infuscated with furcation and cross veins margined with brown.

Variations: (Specimens examined—75) Departures from Stone's (1938) description include the following: frontal index reaching 1:5.6; specimens with narrow frons usually have hind femora mostly dark and cell R_5 closed; fore tibia occasionally unicolorous.

Tabanus sulcifrons is a highly variable species and may actually be composed of a complex of several species. It closely resembles *T. abdominalis* Fabr., and frequently intermediate specimens are difficult to determine. In general, the abdomen of *T. sulcifrons* is not as orange as that of *T. abdominalis*, and in the latter, cell R_5 is closed (see also discussion under *T. abdominalis*). *Tabanus nefarius* Hine and *T. gladiator* Stone are also members of this complex. The variability of this group makes it difficult to rely on any one specific character, but rather a combination of characters must be used to separate these forms.

Ecology and Distribution: (June–October) A late season species, *T. sulcifrons* was locally abundant and an important pest of livestock. It was taken throughout most of the state primarily from the mixed hardwood forests associated with lowland and upland streams and waterways. Hine (1907a) and Jones and Bradley (1924) recorded *T. sulcifrons* and *T. exul* O.S., the latter probably referred to *T. sulcifrons* also.

Mature larva (Fig. 28): Moderate in size, 36–38 mm long; creamy white with extremely pale to light brown pubescent markings.

Head capsule length: 4.3–4.5 mm.

Striations: Present on all aspects of segments except dorsally and ventrally on the thorax where they may be absent, or inconspicuous and broken; striations somewhat finer laterally on the first seven abdominal segments. Striations of the anal segment conspicuous only beyond the anterior ⅓ of the segment.

Thorax: Anterior pubescent annuli with

lateral projections extending about ¾ the length of the pro- and mesothorax, and ½ the length of the metathorax.

Abdominal segments 1–7: Anterior pubescence faint, encircling segments 1–4, becoming progressively reduced on remaining segments. Pseudopodial pubescent rings complete, joined with anterior pubescence dorsolaterally on segments 1–2 and ventrolaterally on 1–5. Faint bands of posterior pubescence encircling all segments, darkest on the preanal segment.

Anal segment: Pubescence consisting of anal and posterior rings connected by a lateral curved arm usually broken for part of its length into isolated pubescent spots; two or three small pubescent spots located dorsolaterally above the arm.

Respiratory siphon: 0.9–1.0 mm, slightly longer than its basal diameter.

Comments: Eight larvae were collected from several localities in St. Landry and East Baton Rouge parishes. The larvae were terrestrial and associated with the moist forest soils of the mixed bottomland hardwood regions. Wilson (1969) also reported taking this species from the forest floor in St. Landry Parish.

Tabanus texanus Hine, 1907

Length 9–14 mm; yellowish brown; eye green with a single reddish purple band; frons 2.5–3 times higher than basal width; antenna yellow-orange with annulate portion black; abdomen with three rows of contiguous pale spots; wing hyaline, costal cell infuscated.

Variations: (Specimens examined—7) Departures from Stone's (1938) description include the following: palpi variable, not especially narrowing to acute apex; femora dark, covered with fine yellowish pollen.

Ecology and Distribution: (May–June) This species was collected with *T. nigrovittatus* Macq. on the coastal marshes of Cameron Parish.

Tabanus trimaculatus Palisot de Beauvois, 1806

Length 15–18 mm; eye uniformly dark; frons usually 4–5 times higher than basal width; thorax grayish; abdomen above blackish with three distinct median white triangles; wing nearly hyaline with furcation and cross veins lightly margined with brown; costal cell infuscated.

Variations: (Specimens examined—250) Departures from Stone's (1938) description include the following: eyes in life or relaxed specimens lacking the two green bands (erroneously recorded by Osten Sacken, 1876); rarely, a small median white spot present on tergite two; rarely, median abdominal triangles reduced.

This species is closely related to *T. superjumentarius* Whit. as is indicated by their similarities in both the adult and larval stages. (For the adult description of *T. superjumentarius*, see Stone, 1938, p. 99.)

Ecology and Distribution: (April–August) This commonly collected species was taken throughout the state primarily from the mixed hardwood forests associated with streams and waterways. It was not taken from the coastal marsh. Hine (1907a) and Jones and Bradley (1924) reported *T. trimaculatus* from Louisiana but indicated that it was seldom collected.

Mature larva (Fig. 30): Moderate in size, 36–42 mm long, creamy white with light to medium brown pubescent markings.

Head capsule length: 4.2–5.1 mm.

Striations: Present laterally on segments 1–10; absent dorsally and ventrally except on the pro- and mesothorax where they are usually present only at posterior margins. Striations encircling anal segment, conspicuous beyond the anterior ⅓ of segment. Extremely fine at the anterior portion where they produce a shadowed effect.

Thorax: Anterior pubescent annuli somewhat broader laterally; lateral surface of prothorax with a pubescent bib, the central portion and lateral arms of which extend about ⅔ and ¾, respectively, the length of the segment. Meso- and metathorax with lateral projections extending at least ¾ the length of the segments; mesothoracic projections slightly expanded apically. A narrow incomplete posterior pubescent band encircles the metathorax.

Abdominal segments 1–7: Anterior pubescence encircling segments 1–5; absent later-

ally on 6 and laterally and ventrolaterally on 7. Pseudopodial pubescent rings complete on all segments and joined with anterior pubescence dorso- and ventrolaterally on segments 1–4 or 5. At least faint traces of posterior pubescence encircling all segments, most distinct on the preanal segment.

Anal segment: Pubescence distinct, consisting of anal and posterior rings, the former joined with a lateral pubescent arm which curves in the midlateral portion of the segment and narrows toward, and only occasionally reaches the posterior ring. Two closely situated pubescent spots, and occasionally a small inconspicuous spot lie dorsolaterally above the arm.

Respiratory siphon: 1.6–1.7 mm long, about twice its basal diameter.

Comments: Fifteen larvae of *T. trimaculatus* were collected from Franklin, St. Landry, and West Feliciana parishes. They were taken from mud in streams, ditches, and temporary ponds in the mixed bottomland hardwood and the mixed pine-hardwood regions. Jones and Bradley (1923) reared this species from larvae taken at the margins of pools and brooks near Baton Rouge.

The larvae of *T. trimaculatus* resemble those of *T. lineola*, but full-grown specimens of the latter are smaller in size and have a relatively shorter respiratory siphon. The larval pubescent pattern of *T. trimaculatus* is also similar to that of *T. superjumentarius*. Based on a single specimen from North Carolina, the latter species exhibits an overall darker pubescent pattern although the anterior pubescence of abdominal segments is less extensive. The lateral pubescent arm on the anal segment reaches the posterior ring and the dorsolateral spots above the arm are united. Immediately anterior to the spots is a somewhat roughened and slightly depressed area in the cuticle which expands anteriorly. Debris may be attached in this region and gives the appearance of a pubescent band.

Tabanus turbidus Wiedemann, 1828

Length 18–25 mm; reddish brown; eye in life brownish purple with two reddish bronze to green bands; frons 5.5–7.5 times higher than basal width; third antennal segment orange-brown; legs uniformly reddish brown; wing veins heavily margined with brown; abdomen with a median row of pale triangles.

This species is similar to *T. equalis* Hine. For discussion of variations, ecology and distribution, see under *T. equalis*.

Tabanus venustus Osten Sacken, 1876

Length 16–20 mm; brown and gray; eye purple with two green bands; frons about three times higher than basal width; abdomen with a median row of pale triangles, and sublateral pale spots on segments 3–6; wing hyaline, distinctly spotted with brown.

Variations: (Specimens examined—25) Departures from Stone's (1938) description include the following: pleura and sternum light tan to predominantly black.

Ecology and Distribution: (May–July) This species was collected from the mixed bottomland hardwood forests of East Baton Rouge, Franklin, and Lafayette parishes and from the mixed pine-hardwood forests of Caddo, Livingston, and Winn parishes. Hine (1907a) reported *T. venustus* from Acadia, DeSoto, and Rapides parishes. Jones and Bradley (1923) collected a larva (reared) from the muddy margin of a brook in East Baton Rouge Parish.

Tabanus wiedemanni Osten Sacken, 1876

Length 17–22 mm; entirely dark brown to black; eye purple with four green bands, the upper band short and parallel to frons; frons 3–4 times higher than basal width; subcallus protuberant and shiny; genae pollinose; wing dark brown.

Ecology and Distribution: This species was not collected in Louisiana by the author. Hine (1907a) reported *T. wiedemanni* from DeSoto Parish (June). However, the description he gave (p. 59) is insufficient to distinguish this taxon from *T. aranti* Hays, and possibly *T. colon* Thun. and *T. nigrescens* P. de B. Jones and Bradley (1923) reported rearing a larva of this species collected beneath standing water in a swampy meadow near Baton Rouge.

Tabanus wilsoni Pechuman, 1962

Length 10–15 mm; brown; eye green with three reddish purple bands; frons 5–6 times higher than basal width; antenna orange-brown, annulate portion black; abdomen with

a median pale stripe expanded posteriorly on each segment, and a sublateral row of pale spots on each side; wing hyaline.

Variations: (Specimens examined—46) Departures from Pechuman's (1962) description include the following: height of frons less than six times its basal width; median callus sometimes reaching basal callus by a very thin line.

Ecology and Distribution: (April–July) This species was collected primarily from the mixed bottomland hardwood forests of the Mississippi and Red river floodplains. Specimens were also taken in upland hardwood forests of West Feliciana Parish. Pechuman (1962) reported that the *T. longiusculus* of Jones and Bradley (1923, 1924) and the *T. fulvulus* (in part) of Hine (1907a) were actually *T. wilsoni.*

Tabanus zythicolor Philip, 1936

Length 11–14 mm; orange-brown; eye in life dull purplish green with two green bands bordered by three purple bands; frons parallel-sided, 3.5–5 times higher than basal width; antenna usually orange; abdomen with a median row of slender contiguous spots and a sublateral row of spots on each side; wing hyaline to subhyaline, costal cell infuscated.

Variations: (Specimens examined—30) Departures from Stone's (1938) description include the following: eye as described above; occasionally basal portion of third antennal segment elongate with only a slight dorsal angle and no dorsal excision; rarely some specimens exhibit the third antennal segment with annulate portion dark—these individuals may be difficult to distinguish from *T. longiusculus* Hine; however, the parallel-sided frons, eye color, and thinner palpi will usually separate *T. zythicolor.*

Ecology and Distribution: (July–October) This late season species was collected from the mixed pine-hardwood region of East Feliciana, St. Helena, and Tangipahoa parishes. A specimen (DeSoto Parish, September) seen by the author in the U.S. National Museum and determined as *T. sagax* by Hine is actually *T. zythicolor.*

Genus Hybomitra Enderlein, 1922

Most Nearctic species of this genus are more northern in distribution. Only four are reported from Louisiana. Members of the genus are rather compact flies usually with a denuded ocellar tubercle and vary in size from small to large. The eyes are usually pilose and the third antennal segment is subdivided into five parts (four annuli).

Hybomitra cincta (Fabricius, 1794)

Tabanus cinctus Fabricius. Stone, 1938, USDA Misc. Publ. 305. p. 125.

Length 18–22 mm; eye purple with four blue-green bands; frons 4–5 times higher than basal width; black with a broad band of orange across base of abdomen; wing dark.

Variations: (Specimens examined—8) Departures from Stone's (1938) description include the following: frontal index ranging to 1:5; antennal color orange-brown to black.

Ecology and Distribution: (May) This very distinctive species was seldom collected. Specimens were taken flying near a small stream in the longleaf-slash pine region of Washington Parish.

Hybomitra difficilis (Wiedemann, 1828)

Tabanus carolinensis Macquart. Stone, 1938, USDA Misc. Publ. 305. p. 126.

Length 12–15 mm; brownish; eye dark purple with four blue-green bands; frons about three times higher than basal width; subcallus denuded and shiny; abdomen with three rows of indistinct spots; wing hyaline, costal cell infuscated.

Variations: (Specimens examined—3) All agree with Stone's (1938) description.

Ecology and Distribution: (April) Three specimens were collected from an upland hardwood forest in West Feliciana Parish.

Hybomitra lasiophthalma (Macquart, 1838)

Tabanus lasiophthalmus Macquart. Stone, 1938, USDA Misc. Publ. 305. p. 128.

Length 11–16 mm; eye noticeably pilose, dark purple with four blue-green bands; frons 3–4 times higher than basal width; thorax dark; abdomen yellow-orange with a middorsal black stripe; wing nearly hyaline, costal cell lightly infuscated; furcation and cross veins margined with brown.

Variations: (Specimens examined—50) All agree with Stone's (1938) description.

Ecology and Distribution: (March–May) This species was collected most frequently in the mixed bottomland hardwood regions associated with the floodplains of major rivers. Six larvae (none reared) were found in the moist forest soils of these regions. The larval habitat was similar to that of *T. proximus* Walk. Wilson (1969) also reported taking this species from the forest floor in St. Landry Parish. Jones and Bradley (1923, 1924) recorded adults of this species from Louisiana under the name of *Tabanus lasiophthalmus.*

Hybomitra trispila (Wiedemann, 1828)

Tabanus trispilus Wiedemann. (in part), Stone, 1938, USDA Misc. Publ. 305. p. 149.

Length 13–16 mm; black; eye purple with four green bands; frons about 3–3.5 times higher than basal width; abdomen with a median row of white triangles; wing dark.

Variations: (Specimens examined—5) Departures from Stone's (1938) description include the following: palpi tan to gray.

Ecology and Distribution: (May) One specimen was taken from a mixed bottomland hardwood region in Natchitoches Parish. Four other specimens were collected from longleaf-slash pine areas in Rapides, St. Tammany, and Washington parishes.

Genus Agkistrocerus Philip, 1941

This genus contains two Nearctic species, one of which, *Agkistrocerus megerlei* (Wiedemann), is reported from Louisiana. *A. finitimus* (Stone) has been taken in Mississippi and Texas and probably occurs in Louisiana also. Members of this genus are rather robust flies with finely pilose eyes, erect black hairs laterally on the subcallus, and the third antennal segment with five divisions, the basal one with a forward projecting hook-like process above.

Agkistrocerus megerlei (Wiedemann, 1828)

Dicladocera megerlei (Wiedemann). Stone, 1938, USDA Misc. Publ. 305. p. 16.

Length 15–21 mm; orange and black; frons about three times higher than basal width; third antennal segment with prominent process; abdomen dull orange with a middorsal black stripe; wing hyaline posteriorly, furcation and cross veins margined with brown.

Variations: (Specimens examined—8) Departures from Stone's (1938) description include the following: vertex of all specimens with black triangular denuded area; occasionally rectangular black denuded area extending from basal callus to top of median callus, not triangular shaped as illustrated by Stone, p. 16; antennae orange-brown, annulate portion and occasionally more than ¾ of distal portion of plate, black; legs dark brown to black; abdomen with a faint median ventral dark line.

Ecology and Distribution: (March–April) This species was collected near small streams and rivers that drain the longleaf-slash pine forests of Florida and Alabama. A single specimen collected from Rapides Parish, Louisiana, in April was provided through the courtesy of Dr. Matt E. Dakin. This species was reported as *Tabanus megerlei* from Ouachita Parish by Hine (1907a).

Genus Hamatabanus Philip, 1941

This genus includes three Nearctic species, two of which, *Hamatabanus annularis* (Hine) and *H. sexfasciatus* (Stone), are rarely collected. Members of the genus have pilose eyes, third antennal segment with five divisions, the basal one usually with a forward projecting hook-like process above; subcallus pollinose lacking the lateral black hairs as found in the *Agkistrocerus.*

Hamatabanus annularis (Hine, 1917)

Dicladocera annularis (Hine). Stone, 1938, USDA Misc. Publ. 305. p. 17.

Length 10–12 mm; brownish; abdomen dark reddish brown above with median ⅓, black; margins of tergites with a band of yellowish gray pollen and hair; wing hyaline, costal cell infuscated.

Variations: A single Louisiana specimen, somewhat damaged, was compared with specimens in the U.S. National Museum. The antennae resembles those of *H. annularis*, although the forward projecting dorsal process of the third antennal segment does not attain the annulate portion. The palpi resemble those of *H. sexfasciatus*, and the basal callus is chestnut brown. The poor condition of the specimen makes positive

determination difficult. Dr. L. L. Pechuman (personal correspondence) indicated that this specimen was probably *H. annularis* although it is larger and darker than the *H. annularis* type series in the Ohio State University collection.

Ecology and Distribution: (April) The single specimen was collected from a mixed pine-hardwood forest in Tangipahoa Parish.

Hamatabanus carolinensis (Macquart, 1838)

Dicladocera scita (Walker). Stone, 1938, USDA Misc. Publ. 305. p. 16.

Length 13–17 mm; brownish; eye deep olive with one dark purple band; abdomen with three rows of pale spots; wing hyaline.

Variations: (Specimens examined—11) Departures from Stone's (1938) description include the following: eye only sparsely pilose in some specimens; frons ratio 1:3 to 1:3.5; occasionally median callus expanded laterally, not slender; the antennal dorsal forward projecting process may or may not be pronounced; annulate portion of third antennal segment shorter than basal portion; costal cell of wing with faint trace of infuscation.

Ecology and Distribution: (April–June) Specimens were collected along small streams in the mixed pine-hardwood regions of East Baton Rouge, East Feliciana, and St. Helena parishes and from the longleaf-slash pine region of Tangipahoa Parish. Jones and Bradley (1923, 1924) reported this species from the state under the name of *Tabanus cerastes* O.S.

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Addendum

Goniops chrysocoma and *Tabanus gladiator* have recently been collected in Louisiana.

Index to Species Accounts

Page

Esenbeckia Rondani
incisuralis (Say)*
Goniops Aldrich
chrysocoma (Osten Sacken) 93
Merycomyia Hine 38
whitneyi (Johnson)* 38
Silvius Meigen 39
quadrivittatus (Say) 39
Chrysops Meigen 39
abatus Philip 39
amazon hubbelli Philip 41
atlanticus Pechuman 41
beameri Brennan 42
bistellatus Daecke 42
brimleyi Hine 42
brunneus Hine 44
callidus Osten Sacken 44
carbonarius Walker 45
celatus Pechuman 45
cincticornis Walker 46
cursim Whitney 46
dacne Philip 48
dimmocki Hine 48
dorsovittatus Hine*
flavidus Wiedemann 49
fuliginosus Wiedemann*
fulvistigma Hine 49
geminatus geminatus Wiedemann 51
geminatus impunctus Krober 51
harmani n. sp. 52
hinei Daecke*
hyalinus Shannon*
macquarti Philip 52
moechus Osten Sacken 54
montanus Osten Sacken 54
niger Macquart 54
nigribimbo Whitney 56
obsoletus obsoletus Wiedemann 56
obsoletus lugens Wiedemann 57
parvulus Daecke 57
pikei Whitney 57
pudicus Osten Sacken 58
reicherti Fairchild 58
sackeni Hine*
separatus Hine 60
sequax Williston 60
striatus Osten Sacken 60
tidwelli Philip & Jones*

Page

univittatus Macquart 60
upsilon Philip 62
vittatus Wiedemann 63
Diachlorus Osten Sacken 64
ferrugatus (Fabricius) 64
Stenotabanus Lutz 64
magnicallus (Stone) 64
Chlorotabanus Lutz 64
crepuscularis (Bequaert) 64
Whitneyomyia Bequaert 65
beatifica atricorpus Philip 65
Leucotabanus Lutz 65
annulatus (Say) 65
Tabanus Linnaeus 66
aar Philip 66
abdominalis Fabricius 66
acutus (Bigot) 67
americanus Forster 67
aranti Hays 67
atratus Fabricius 68
calens Linnaeus 69
cheliopterus Rondani 69
coarctatus Stone 69
colon Thunberg 70
cymatophorus Osten Sacken 70
eadsi Philip 70
endymion Osten Sacken 70
equalis Hine 71
exilipalpis Stone*
fairchildi Stone 71
fulvulus Wiedemann 72
fuscicostatus Hine 72
gladiator Stone 93
gracilis Wiedemann*
imitans Walker 73
kisliuki Stone*
lineola lineola Fabricius 74
lineola hinellus Philip 75
longiusculus Hine 75
maculipennis Wiedemann 75
melanocerus Wiedemann 76
moderator Stone 77
molestus Say 77
mularis Stone 79
nefarius Hine 79
nigrescens Palisot de Beauvois* 79
nigripes Wiedemann 80
nigrovittatus Macquart 80
pallidescens Philip 81
petiolatus Hine 82
proximus Walker 82

* Species from neighboring states but not reported from Louisiana (included in key).

	Page
pumilus Macquart	83
quaesitus Stone	83
quinquevittatus Wiedemann*	83
reinwardti Wiedemann	84
rufofrater Walker	84
sackeni Fairchild*	
sagax Osten Sacken	84
sparus Whitney*	
sparus milleri Whitney	85
stygius Say	85
sublongus Stone	86
subsimilis Bellardi	86
sulcifrons Macquart	86
superjumentarius Whitney*	
texanus Hine	87
trijunctus Walker*	
trimaculatus Palisot de Beauvois	87
turbidus Wiedemann	88
venustus Osten Sacken	88
wiedemanni Osten Sacken	88
wilsoni Pechuman	88
zythicolor Philip	89
Hybomitra Enderlein	89
cincta (Fabricius)	89
difficilis (Wiedemann)	89
hinei (Johnson)*	
lasiophthalma (Macquart)	89
trispila (Wiedemann)	90
Agkistrocerus Philip	90
finitimus (Stone)*	90
megerlei (Wiedemann)	90
Hamatabanus Philip	90
annularis (Hine)	90
carolinensis (Macquart)	91
sexfasciatus (Stone)*	

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THE SYSTEMATICS AND EVOLUTION OF THE GENUS *CHIROSTOMA* SWAINSON (PISCES, ATHERINIDAE)

CLYDE D. BARBOUR
Department of Biology, University of Utah,
Salt Lake City, Utah 84112

p. 97

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TULANE STUDIES IN ZOOLOGY AND BOTANY

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THE SYSTEMATICS AND EVOLUTION OF THE GENUS *CHIROSTOMA* SWAINSON (PISCES, ATHERINIDAE)

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ABSTRACT

The genus *Chirostoma* is composed of 18 species and six subspecies not including *C. compressum*, thought to be extinct. Except for a few populations of *C. jordani* near Durango City, Durango, it is restricted to the Mesa Central of Mexico where it makes up approximately 20 percent of the fish fauna.

The following names in current usage are herein synonymized: *Otalia* = *Chirostoma*; *C. ocampoi*, *C. regani* = *C. humboldtianum*; *C. diazi* = *C. sphyraena*; *C. ocotlanae* = *C. lucius*. No subspecies of *C. jordani* are recognized. *C. reseratum* is recognized as a subspecies of *C. consocium*. The name *C. attenuatum* Meek is reapplied to the populations in Lakes Pátzcuaro and Zirahuén currently designated as *C. bartoni*. Five individuals from the lake at Balneario Cointzio, Michoacán are referred to *C. charari* De Buen. *C. **aculeatum*** is described as new.

Chirostoma is divided into two species groups. The jordani group generally has high meristic values, the lateral line scales with canals, scales with laciniate margins and includes *C. jordani*, *C. patzcuaro*, *C. chapalae*, *C. consocium*, *C. humboldtianum*, *C. estor*, *C. grandocule*, *C. lucius*, *C. sphyraena* and *C. promelas*. The arge species group generally has low meristic values, the lateral line scales with round pores (except for the last two species named below) and scales with smooth margins and includes *C. arge*, *C. melanoccus*, *C. charari*, *C. riojai*, *C. bartoni*, *C. attenuatum*, *C. labarcae* and *C. aculeatum*.

The similarity between *C. arge* and *Melaniris crystallina* and the primitive nature of *C. jordani* is noted. The evolution of *Chirostoma* is best explained by considering the genus to be diphyletic; a *Menidia*-like ancestor of the jordani group invaded the Mesa Central first, followed at a later time by the *Melaniris*-like ancestor of the arge group. The evolution of the species is summarized in a hypothetical phylogenetic tree.

CONTENTS

INTRODUCTION 98
METHODS 98
ACKNOWLEDGMENTS 99
DIAGNOSTIC CHARACTERS 100
KEY TO SPECIES OF THE GENERA *Chirostoma* AND *Melaniris* 101
THE JORDANI GROUP 102
Chirostoma jordani 102
Chirostoma patzcuaro 107
Chirostoma chapalae 107
Chirostoma humboldtianum 108
Chirostoma consocium consocium 110
Chirostoma consocium reseratum 110
Chirostoma grandocule 112
Chirostoma compressum 114
Chirostoma estor estor 114
Chirostoma estor copandaro 116
Chirostoma lucius 118
Chirostoma sphyraena 118
Chirostoma promelas 120
THE ARGE GROUP 120
Chirostoma arge 122
Chirostoma melanoccus 122
Chirostoma riojai 122
Chirostoma charari 126

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Chirostoma attenuatum attenuatum 128
Chirostoma attenuatum zirahuen 128
Chirostoma bartoni 129
Chirostoma labarcae 129
Chirostoma ***aculeatum*** 130
PHYLOGENY OF *Chirostoma* 131
PRIMITIVE AND DERIVED CHARACTERS 131
PRIMITIVE SPECIES WITHIN THE SPECIES GROUPS 132
POSSIBLE ANCESTORS AND THE ORIGIN OF *Chirostoma* 133
EVOLUTION WITHIN THE SPECIES GROUPS 137
CONCLUSIONS 138
RESUMEN 139
LITERATURE CITED 140

INTRODUCTION

The Republic of Mexico, by reason of its geographic position and geological history, possesses a large and interesting fish fauna. The coastal lowlands have served as avenues of migration for North and Central American fishes and contain mixed faunas reflecting strong affinities for these regions. On the other hand, the uplifted, central portion of the country, from the transverse volcanic axis northward, contains a large number of unique species. The fishes present in the basins of the north show clear but varying degrees of relationship with the Rio Grande fauna. On the southern one-third of the pleateau, however, in the westward flowing Lerma-Santiago river system and contiguous fluvial and lacustrine basins, endemism reaches generic and familial levels.

Chirostoma is one of the unique groups in this evolutionary microcosm. The genus has been reviewed or revised several times, most notably by Jordan and Evermann (1895; 1896–1900), Meek (1904), Regan (1906–1908), Jordan and Hubbs (1919) and De Buen (1945). Through the years the number of species has steadily increased as well as the confusion regarding their relationships. Jordan and Evermann (1895) placed the species into two genera: *Chirostoma*, characterized as having the snout slightly produced, small teeth, an oblong body and a small first dorsal fin placed over the vent and *Eslopsarum*, being close to *Chirostoma*, but with large and entire scales. Jordan and Evermann (1896–1900) erected a third genus, *Lethostole*, for *C. estor* characterized as having thin, translucent, pale flesh and differences in the firmness of its scales and bones. The same authors later decided (Jordan and Evermann, 1896–1900, Vol. 4, p. 3158) that *Lethostole* was not separable from *Chirostoma*. Meek (1904) recognized one genus and allocated the species among three subgenera: *Chirostoma*, *Eslopsarum* and *Lethostole*. Regan (1906–08) and Jordan and Hubbs (1919) could find no consistent method by which the species could be grouped and so recognized no subgenera. Jordan, Evermann and Clark (1930) followed Meek (1904). De Buen (1945) distributed the species among three genera and six subgenera. Alvarez (1950, 1970) recognized two genera in his keys, *Chirostoma* and the monotypic *Otalia*.

The objectives of this paper are to redefine the species which have been included in *Chirostoma* and to discuss their evolutionary relationships. No attempt has been made, however, to diagnose the genus because little comparative data is available for most of the other atherine genera. Patterns of morphological variation within the family (Rosen, 1964) are not yet clear. This somewhat unorthodox presentation is also justified by the biogeographic history of *Chirostoma*, a topic to be discussed in another paper.

METHODS

Counts and measurements were made in accordance with Hubbs and Lagler (1958) in most instances. Where these methods were in appropriate they were modified or new characters used as described below.

The number of median lateral scales was considered to be the number of scales in a series extending from the scapular arch dorsal and anterior to the insertion of the pectoral fin to the end of the hypural plate. The count includes scales which may be reduced in size just posterior to the head. The predorsal scale count was made along an imaginary line between the origin of the first dorsal fin and the head and included, when present, the large scale which usually has its origin on the head, but lies on the nape. Only those scales intersecting the line by at least one-half a scale width were counted. The interdorsal scales, the number of scales in a series lying between the scale upon which the first dorsal fin membrane

inserts and the origin of the second dorsal fin, were counted in the same manner as the predorsals.

The condition of the scale margins and the type of lateral line pore were also found to be useful characters. The former are either smooth (entire) or laciniate (toothed or crenulate). The openings in the scales of the lateral line system are either horizontally elongate (canals) or round (pores).

Nineteen morphometric and nine meristic characters were examined in each of the species of *Chirostoma* over their known ranges and in *Menidia berylina* (Grand Isle, Louisiana) and *Melaniris crystallina* (Río Grande de Santiago at Hwy 15 crossing, Nayarit). Wherever possible body proportions were measured on twenty adult individuals and fifty or more were examined meristically. However, sample sizes were occasionally determined by the availability of specimens. Ranges, means, 95 percent confidence intervals of the means and standard deviations were computed for each character for all samples of more than six specimens and plotted on graph paper according to the method of Hubbs and Hubbs (1953). Each chart was copied, cut apart, and the populations or species arranged in different ways to reveal geographic or phylogenetic trends and patterns. Characters which clearly show trends or patterns important to the understanding of the evolution of *Chirostoma* are presented in Figs. 5–15. Unless otherwise stated, the statistical analyses were performed on pooled data taken from specimens over the known ranges of the species.

Life colors given in the text were observed in the field from living specimens. Pigmentation patterns were more easily examined in the laboratory and were recorded from preserved specimens.

The synonymies are given in abbreviated form with the complete references listed under Literature Cited.

Base maps (semi-diagrammatic) on which distributions are plotted were compiled from appropriate sheets of the Mapa de los Estados Unidos Mexicanos (1:500,000) published by the Comisión Intersecretarial Coordinadora del Levantamiento de la Carta Geographica de la Republica Mexicana (1957), the Map of North America (1:1,000,000) published by the American Geographical Society (1935), the road atlas, *Caminos de México*, published by La Compania Hulera Euzkadi (third edition, 1967) and from my own observations. Where more than one collection was taken from a specific locality, only one is shown on the map. Questionable locality records are not plotted on the maps, but are discussed in the text under *Range*.

The following abbreviations appear in this paper: ca. (circa), about; ft., feet; hwy., highway; jct., junction; km, kilometer; mi., miles; trib., tributary. Geographic directions are indicated by the initial letters of the cardinal points of the compass, North, South, East, West or various combinations thereof.

Acknowledgments

The majority of the specimens forming the basis for this study were taken during the summer of 1963 and during the springs of 1964 and 1969 by collecting parties from Tulane University and the University of Utah and over the past 15 years by Robert R. Miller and his associates and students at the University of Michigan. This material is housed largely at Tulane University (TU) and at the University of Michigan Museum of Zoology (UMMZ) under the care of Royal D. Suttkus and Robert R. Miller and Reeve M. Bailey respectively. I am deeply grateful to these individuals for their prompt assistance in the loan of material and other courtesies too numerous to mention.

It would not have been possible to complete this work without the examination of specimens deposited in other museums and universities. The following persons kindly allowed me to examine collections entrusted to their care and assisted me in numerous ways: José Alvarez, Instituto Politecnico Nacional, México, D. F. (P); James E. Böhlke, Academy of Natural Sciences of Philadelphia (ANSP); Salvador Contreras, Facultad de Ciencias Biológicas, Universidad de Nuevo León, México (FCB); P. Humphry Greenwood, British Museum of Natural History (BM); George S. Myers and Warren C. Freihofer, Division of Systematic Biology, Stanford University (SU), recently moved to the California Academy of Sciences; Wilbur I. Follett and William P. Eschmeyer, California Academy of Sciences (CAS); Leonard P. Schultz and Ernest A. Lachner, National Museum of Natural History, Smithsonian Institution (USNM);

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Thanks go to Salvador Contreras for enduring two field trips to Mexico with me and for translating my summary into Spanish. Aurelio Solórzano extended the hospitality of his laboratory in Mexico City and arranged for the use of the facilities of the Limnological Station at Pátzcuaro, Michoacán. Successful collecting in Lake Pátzcuaro and the surrounding area was due to the enthusiastic cooperation of Juan Pizá, former caretaker of the Limnological Station. José Alvarez generously shared his knowledge of the fishes of central Mexico with me and directed me to several important localities. Finally, I would like to thank the Departamento de Estudios Biólogicos Pesqueros for issuing me permits to collect in Mexico.

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Diagnostic Characters

Single characters or character complexes which are critical for the separation of species are rare in *Chirostoma.* Most of the characters discussed below are diagnostic only in various combinations with themselves. Their utility for differentiating between the species groups is not discussed.

Meristic characters.—The following meristic characters are compared in Figs. 5–10: median lateral, predorsal and interdorsal scales, pectoral and anal fin rays, gill rakers and vertebral numbers. First and second dorsal fin rays were also examined, but did not vary sufficiently to be of use.

Geographic variation was found in certain meristic characters and is discussed following the descriptive data of the appropriate species.

Morphometric characters.—Nineteen morphometric characters were analyzed for this study. The most useful are compared in Figs. 11–14: head length, mandibular length, snout to first dorsal fin origin and anal fin height. In certain instances the following measurements aided in differentiating between species: snout to the origins of the second dorsal, anal and pelvic fins, snout, eye, pectoral fin, postorbital head lengths, lengths of the caudal peduncle and the base of the anal fin, least depth of the caudal peduncle, and the height of the second dorsal fin. Four measurements were found to be of no use for separating the species of *Chirostoma*: lengths of the second dorsal fin base and the pelvic fins, greatest body depth and the fleshy interorbital width.

All morphometric characters showed some degrees of allometric growth. When juvenile to adult specimens of all the species are available for study in adequate numbers, more accurate diagnoses will be able to be

written. Until that time care should be taken in the identification of subadults.

Pigmentation.—The distribution and concentration of melanophores over the body is usually highly variable and dependent on the clarity of the water in which the species or population lives. In a few instances, however, concentrations of pigment cells occur independently of environmental conditions and are useful for distinguishing species.

Dentition.—All species of *Chirostoma* have conical teeth. However, tooth size and placement showed important interspecific differences.

Scales.—The types of scale edge and lateral line opening described under METHODS are most useful for differentiating between the species groups although occasionally they may separate species within a group. The degree of scale edge laciniation shows pronounced intraspecific variation in one case.

Key to Species of the Genera *Chirostoma* and *Melaniris*[1]

1a. Lateral line scales with pores only ... 2
b. Lateral line scales with canals only or pores and canals present on the same specimen ... 9
2a. Length of anal fin base, 28.7–32.6 in percent of standard length; length of pectoral fin, 22.2–28.2; length of caudal peduncle 15.2–19.2 ... *M. crystallina*
b. Length of anal fin base, 14.9–24.4; length of pectoral fin, 12.9–18.8; length of caudal peduncle, 21.4–30.2 ... 3
3a. Teeth large; teeth present on premaxillary outside the mouth and easily seen or felt when mouth is closed ... *C. arge* (See also 26a)
b. Teeth large or small; teeth on premaxillary not outside the mouth ... 4
4a. Premaxillaries project strongly anteriorly, sharply decurved ... *C. charari*
b. Premaxillaries do not project strongly anteriorly, not sharply decurved ... 5
5a. Gill rakers, 12–18 ... 6
b. Gill rakers, 19–26 ... 7
6a. Length of eye, 5.1–6.0 ... *C. riojai*
b. Length of eye greater than 6.0 ... 7
7a. Median lateral scales, 39–45; gill rakers, 17–22; distance from snout to first dorsal fin, 48.1–51.9 ... *C. melanoccus*
b. Median lateral scales, 42–70; gill rakers, 20–26; distance from snout to first dorsal fin, 44.9–50.3 ... 8
8a. Median lateral scales, 42–49; distance from snout to first dorsal fin, 47.4–50.3; length of caudal peduncle, 22.3–24.9; snout angular in profile ... *C. bartoni*
b. Median lateral scales, 43–51; distance from snout to first dorsal fin, 43.1–46.2; length of caudal peduncle, 26.6–30.2; snout blunt to angular, usually the latter ... *C. attenuatum attenuatum*
c. Median lateral scales, 48–70 (rarely 48 or 49); distance from snout to first dorsal fin, 44.4–48.9; length caudal peduncle, 23.9–30.1; snout blunt to subtriangular ... *C. attenuatum zirahuen*
9a. Snout black or partially so; lower jaw equal to or included by upper jaw ... *C. promelas*
b. Snout not black, does not include lower jaw ... 10
10a. Teeth small; lower jaw may project strongly beyond snout ... 11
b. Teeth large; some may be canine-like; lower jaw may project strongly beyond snout or snout may be subtriangular to pointed (barracuda-like) ... 25
11a. Median lateral scales with entire edges, rarely laciniate ... *C. jordani*
b. Median lateral scales laciniate ... 12
12a. Gill rakers, 28–34 ... 13
b. Gill rakers, 19–28 ... 14
13a. Median lateral scales, 58–77; anal rays, 18–22; length caudal peduncle, 21.2–23.5; height of second dorsal fin, 13.3–14.8 ... *C. grandocule*
b. Specimen does not fit description in 13a ... 14
14a. Snout length, 7.2–9.5 ... 15
b. Snout length, 9.6–12.5 ... 21
15a. Median lateral scales, 44–55 ... 16
b. Median lateral scales, 52–69 ... 17
16a. Head length, 23.9–25.5; postorbital head length, 10.7–12.0; snout length, 7.3–8.1; jaw length, 8.6–9.4 ... *C. chapalae*

[1] *Chirostoma compressum*, thought to be extinct, is not included in the key.

b. Head length, 25.6–34.2; postorbital head length, 12.2–16.8; snout length, 8.4–13.4; jaw length, 9.5–15.0 ..... *C. humboldtianum* (See also 20b, 22a)

17a. Predorsal scales, 24–34 18

b. Predorsal scales, 33–79 19

18a. Head length, 24.5–25.9; postorbital head length, 11.2–12.5; snout length, 7.5–8.7; jaw length, 8.8–9.9; length of caudal peduncle, 23.7–25.6; snout slightly pointed ..... *C. patzcuaro*

b. Specimen does not fit description in 18a 16b

19a. Predorsal scales, 33–56 20

b. Predorsal scales, 43–79 ..... *C. consocium consocium*

20a. Gill rakers, 23–30 ($\bar{x}$ = 27); snout to pelvic fin origin, 39.7–43.3 ($\bar{x}$ = 41.0); length of anal fin base, 20.2–23.2 ($\bar{x}$ = 21.4) ..... *C. consocium reseratum*

b. Gill rakers, 19–28 ($\bar{x}$ = 23); snout to pelvic fin origin, 40.9–51.2 ($\bar{x}$ = 44.0); length of anal fin base, 17.1–22.2 ($\bar{x}$ = 19.4) ..... *C. humboldtianum* (See also 16b, 22a)

21a. Predorsal scales, 24–50 22

b. Predorsal scales, 50–117 23

22a. Median lateral scales, 47–73 ($\bar{x}$ = 60) ..... *C. humboldtianum* (See also 16b, 20b)

b. Median lateral scales, 67–86 ($\bar{x}$ = 75) ..... *C. estor copandaro* (See also 23b)

23a. Mandible length, 12.2–17.9 24

b. Mandible length, 10.3–12.2 (based on small specimens) ..... *C. estor copandaro* (See also 22b)

24a. Median lateral scales, 52–76; mandible length, 13.1–17.9; length of anal fin base, 19.2–23.4; lower jaw may protrude beyond snout by as much as one-half the interorbital distance; teeth may be small or large ..... *C. lucius* (See also 28b)

b. Median lateral scales, 65–90; mandible length, 12.2–14.8; length of anal fin base, 16.1–21.0; lower jaw does not protrude beyond snout; teeth always small ..... *C. estor estor*

25a. Gill rakers, 14–20 26

b. Gill rakers, 23–28 28

26a. Snout blunt; teeth on upper lip, easily seen or felt when mouth is closed; fins may be pigmented black ..... *C. arge* (See also 3a)

b. Snout pointed; no teeth on upper lip; anal fin rays, 18–23 27

27a. Snout strongly pointed; premaxillaries sharply decurved leaving gap in bite when mouth is closed; head length, 27.9–29.8; snout length, 10.1–12.1; mandible length, 12.5–14.5 ..... *C. aculeatum*

b. Snout pointed; no gap in bite when mouth is closed; head length, 23.5–27.1; snout length, 8.3–9.9; mandible length, 9.9–11.7 ..... *C. labarcae*

28a. Snout pointed, narrow; lower jaw projects only slightly beyond snout; interdorsal scales, 8–29 ($\bar{x}$ = 18) ..... *C. sphyraena*

b. Snout blunt, wide; lower jaw may project up to one-half the interorbital distance beyond the snout; interdorsal scales, 6–17 ($\bar{x}$ = 10) ..... *C. lucius* (See also 24a)

The Jordani Group

Description.—Lateral line scales usually with canals; scale margins usually laciniate; median lateral scales, 36–90; predorsal scales, 16–136; interdorsal scales, 0–29; gill rakers, 14–34; vertebrae, 35–47; pectoral fin rays, 10–18; anal fin rays, 14–24. The species range in size from small to the largest of all *Chirostoma* and include: *C. jordani*, *C. patzcuaro*, *C. chapalae*, *C. consocium*, *C. humboldtianum*, *C. estor*, *C. grandocule*, *C. lucius*, *C. sphyraena* and *C. promelas*.

CHIROSTOMA JORDANI WOOLMAN

Fig. 16a

Chirostoma jordani Woolman, 1894:62, Pl. 2, lectotype: USNM 125441, type locality: Río Lerma and canals at Salamanca, Guanajuato; Bean, 1898:540; Meek, 1902:112, 1903:783, 1904:169, Fig. 52; Regan, 1906–08:59, Tab. 10, Fig. 3 (in part); Jordan and Hubbs, 1919:70, Pl. 6, Fig. 21; Jordan, Evermann and Clark, 1928:250; Cuesta Terron, 1931:238; Martin del Campo, 1936:272; De Buen, 1940a:306, 1940c:48, 1941c:7, 1943:212; Alvarez, 1950b:92, 1953:98, 1963:129; Alvarez and Navarro, 1957:8, 16, 50; Alvarez and Cortés, 1962:122. *Chirostoma brasiliensis*, Jordan, 1879:299. *Atherinichthys brevis* Steindachner, 1894:49. *Chirostoma breve*, Von Bayern and Steindachner, 1895:526, Pl. 2, Fig. 2; Regan, 1906–08:59, Tab. 10, Fig. 3 (in part). *Eslopsarum jordani*, Jordan and Evermann, 1895:330, 1896–1900:2840, Fig. 335; Jordan and Snyder, 1899:133; Evermann

and Goldsborough, 1900:152. *Chirostoma mezquital* Meek, 1904:170, Fig. 53; Jordan and Hubbs, 1919:70, Fig. 20; Cuesta Terron, 1931:238; Jordan, Evermann and Clark, 1928:250; De Buen, 1940c:48; Martin del Campo, 1940:483. *Eslopsarum jordani mezquital*, De Buen, 1945:503, 1946b:114, 1947: 282. *Chirostoma jordani mezquital*, Schultz, 1948:32; Alvarez, 1950a:101, 1970:124. *Eslopsarum jordani jordani*, De Buen, 1945:501, 1946b:113, 1947:302. *Chirostoma jordani jordani*, Schultz, 1948:31; Alvarez, 1950a:101, 1970:123; Alvarez and Navarro, 1957:43. *Chirostoma hidalgoi*, Alvarez, 1953:25.

Diagnosis.—Median lateral scales, 36–48; gill rakers, 14–22; distance from snout to anal fin origin, 49.0–58.2, $\bar{x} = 53.3$ in percent of standard length; snout length, 4.8–9.8; length of caudal peduncle, 18.6–26.2; height of second dorsal fin, 13.4–22.2, $\bar{x} = 18.3$; length of anal fin base, 18.0–32.4; teeth small to minute, not visible when the mouth is closed, snout usually angular in profile; lateral line scales with either round pores or canals, often on the same specimen with the former predominating; scales on the sides of the body usually with entire edges, laciniate scales present in the predorsal region in large adult specimens (see also below under *Variation*).

Description.—Maximum length for species approximately 70 mm S.L., one specimen from Lake Chapala was 91 mm; body slender to moderately deep; mouth small, oblique, teeth in one or two rows or in a narrow band on premaxillaries and in two rows or a wider band on dentaries, none on vomer or palatines; pectoral fins moderately long and rounded; melanophores faintly concentrated along the posterior margin of the caudal fin in many populations.

Remarks.—Lectotype herein designated, USNM 125441; paralectotypes, USNM 47509 (2), USNM 203104 (1), UMMZ 187660 (1), UMMZ 187661 (1), FMNH 6770 (5), SU 788 (4), CAS 14250 (2), BM 1894 1.27 (7). *C. jordani* was described from a series collected by Woolman and Cox during the summer of 1891. No type was designated, although the description was clearly based on specimens taken from the Río Lerma at Salamanca, Guanajuato. Additional specimens were mentioned as having been collected from canals at Salamanca and from the City of Mexico. The text was accompanied by an illustration of a specimen from Mexico City and presumably was the reason for Jordan and Hubbs' (1919) restriction of the type locality to the Valley of Mexico. As the populations in this basin are slightly different from those found in the Lerma drainage, I here designate the canals and the Río Lerma at Salamanca as the type locality. Unfortunately, the locality on the labels with the type specimens is merely "Salamanca" making it impossible to differentiate between those taken in the canals and in the river.

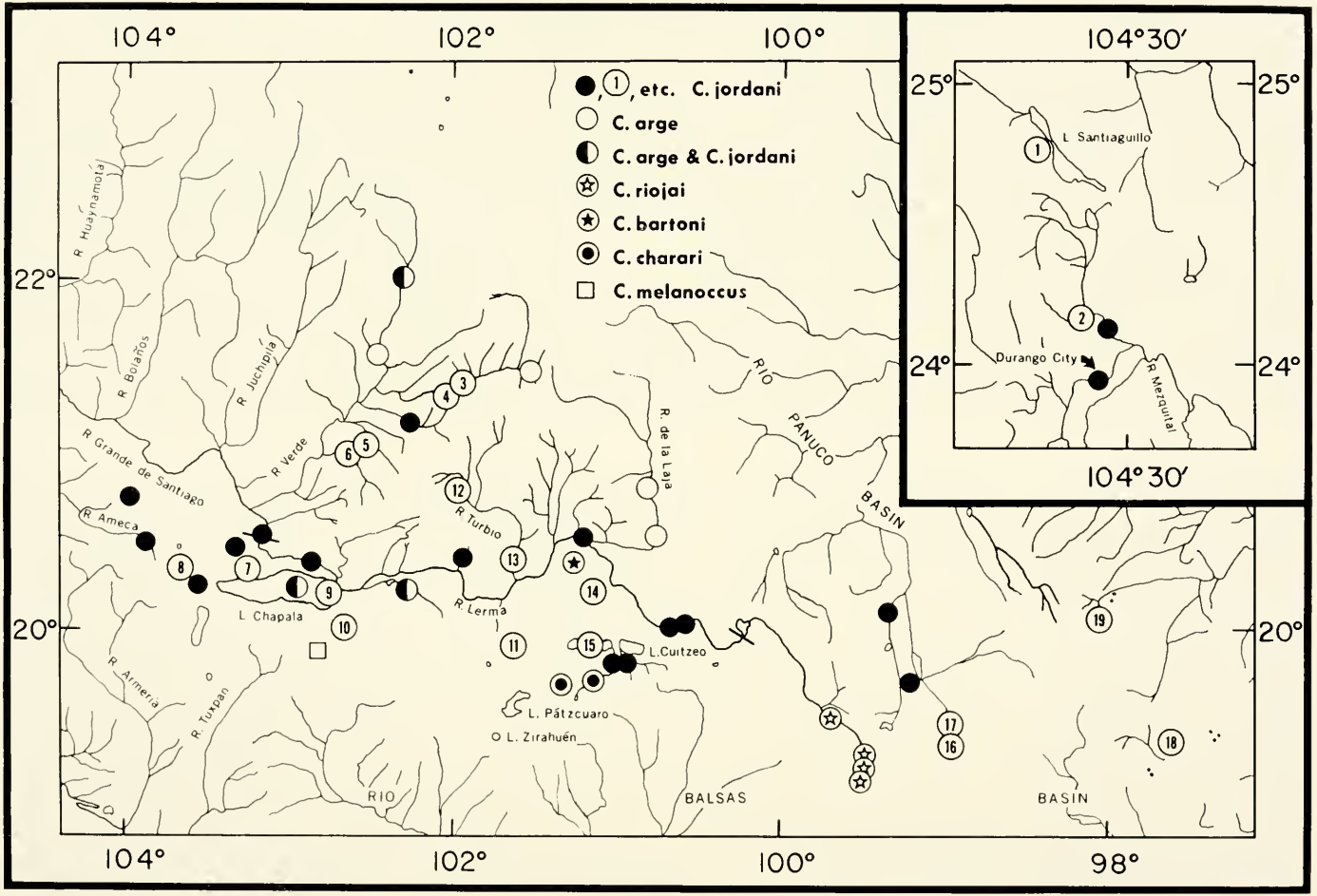
C. jordani was taken from small ponds and streams as well as from the main channel of the Río Santiago and some of the larger lakes. In most cases the species was found associated with vegetation, either drowned terrestrials along the margins of flooded ponds, in and around dense stands of *Scirpus* or under and at the margins of mats of water hyacinth (*Eichornia* sp.). Specimens collected from the Río Santiago at Poncitlán (TU 37759) on July 10, 1963 were spawning and depositing their eggs among the roots of the floating hyacinths.

Variation.—Certain characters are variable over the range of *C. jordani.* Most noticeable are changes in the angularity of the snout and body depth. Most specimens have a very angular snout in lateral view, but large individuals from the Río Grande de Santiago at Poncitlán, Lake Chapala, the Valley of Mexico, El Carmen, Tlaxcala and the Santiaguillo basin north of Durango City, Durango have very blunt snouts. A few individuals from Lake Cuitzeo (UMMZ 172189) share this characteristic. Specimens taken from the above localities, except Lake Cuitzeo, also show a deeper and more robust body.

The number of median lateral and predorsal scales are the only characters demonstrating a pattern of variation (Figs. 2, 3). The recognition of subspecies is not warranted because of the rather uniform differences between the populations. The population in eastern Hidalgo rather than those from the Valley of Mexico or Durango appears to be the most highly differentiated.

The degree of scale laciniation is fairly consistent throughout the range of the species except for the population in eastern Hidalgo. All large individuals collected here had strongly laciniate scales on the sides of the body as well as predorsally.

Range.—Widely distributed on the Mesa Central (Fig. 1). I have not been able to


104°
102°
100°
98°
22°
20°
●, ①, etc. C. jordani
○ C. arge
◐ C. arge & C. jordani
☆ C. riojai
★ C. bartoni
◉ C. charari
□ C. melanoccus
R Huaynamota
R Bolaños
R Juchipila
R Verde
R Grande de Santiago
R Ameca
L Chapala
R Lerma
R Turbio
R. de la Laja
RIO PANUCO BASIN
L.Cuitzeo
L. Pátzcuaro
O L. Zirahuén
R Armeria
R Tuxpan
RIO BALSAS BASIN
104°30′
25°
24°
L Santiaguillo
Durango City
R Mezquital

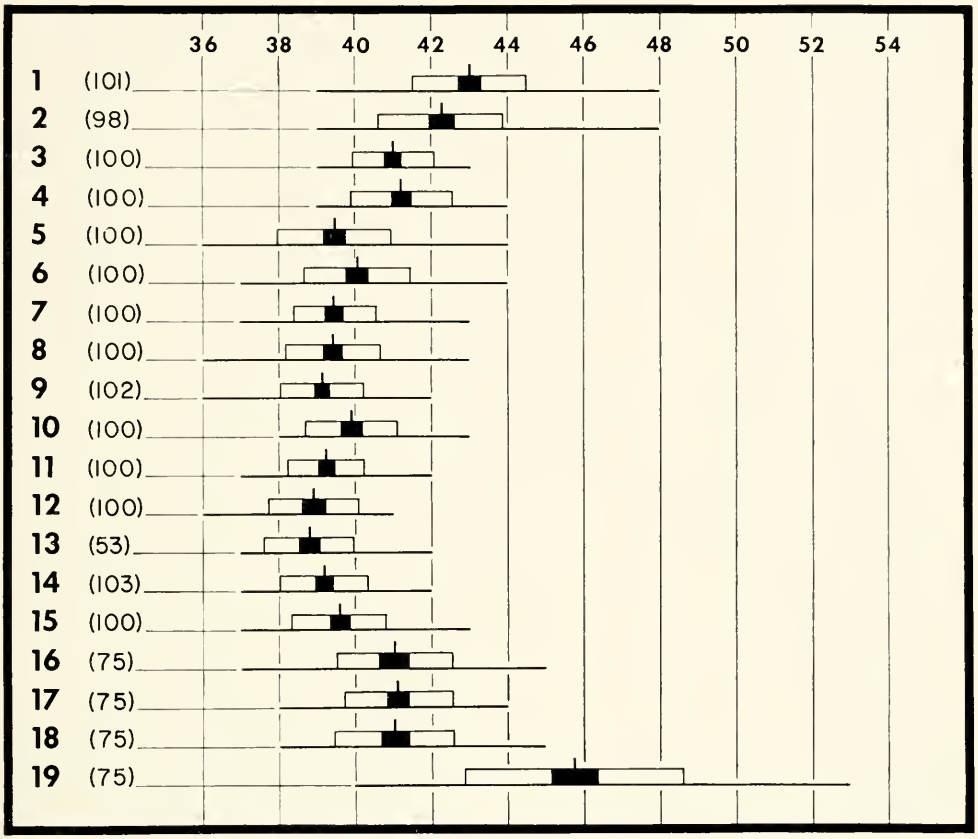


Figure 2. Variation in the number of median lateral scales in *Chirostoma jordani*. For localities and explanation of the diagrams see legends of Figs. 1 and 5.

verify the presence of *C. jordani* in the Balsas system (De Buen, 1945) or recollect this species in the volcanic caldera "La Alberca," Guanajuato. Six specimens were reportedly obtained from the latter locality by A. Dugès, a resident of the city of Guanajuato and cataloged in the U.S. National Museum of Natural History in 1879 (USNM 23135).

Material examined.—The numbers in boldface (1–19) preceding some of the collections correspond to the numbers in Figs. 2, 3. Aguascalientes: FMNH 3581 (7), SU 6178 (2), Río Verde at Aguascalientes. Durango: FMNH 4389, holotype of *Chirostoma mezquital*, Río Mezquital at Durango; ANSP 90855 (1), paratype of *C. mezquital*, Río Mezquital at Durango, out of FMNH 4390; **2**, FCB 484 (1073), TU 40108 (50), TU 37746 (230), at bridge over creek at Guatimapé; TU 40107 (107), **1**, FCB 473 (909), TU 37745 (3289), Presa Peña del Aguila on Río Veintidos ca. 12 mi. N Durango City on hwy. 45 (at Km 1069); CAS 13591 (58), Río Canatlán, trib. of Río Mezquital 22 km N Durango; CAS 13592 (32), Río de Santiago, trib. of Río Mezquital at hwy. crossing 11 mi. E of Durango; USNM 132488 (12), Durango; UMMZ 197644 (12), Río Mezquital and adjacent spring-fed ponds, 9 mi. NE Du-

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Figure 1. Distribution of six species of *Chirostoma* on the Mesa Central of Mexico. Not all collections at a given locality or within a lake are shown. Lake Chapala species probably occur also in adjacent parts of the Río Lerma and the Río Grande de Santiago. Numbers marking localities of *C. jordani* correspond to the boldface numbers in Figs. 2 and 3 and to those preceding the catalogue numbers in the *Material Examined* section for this species. The solid lines across the Lerma-Santiago river indicate the locations of, west to east, the waterfalls at Juanacatlán and below Tepuxtepec dam. Abbreviations: L., Lake; R., Río.

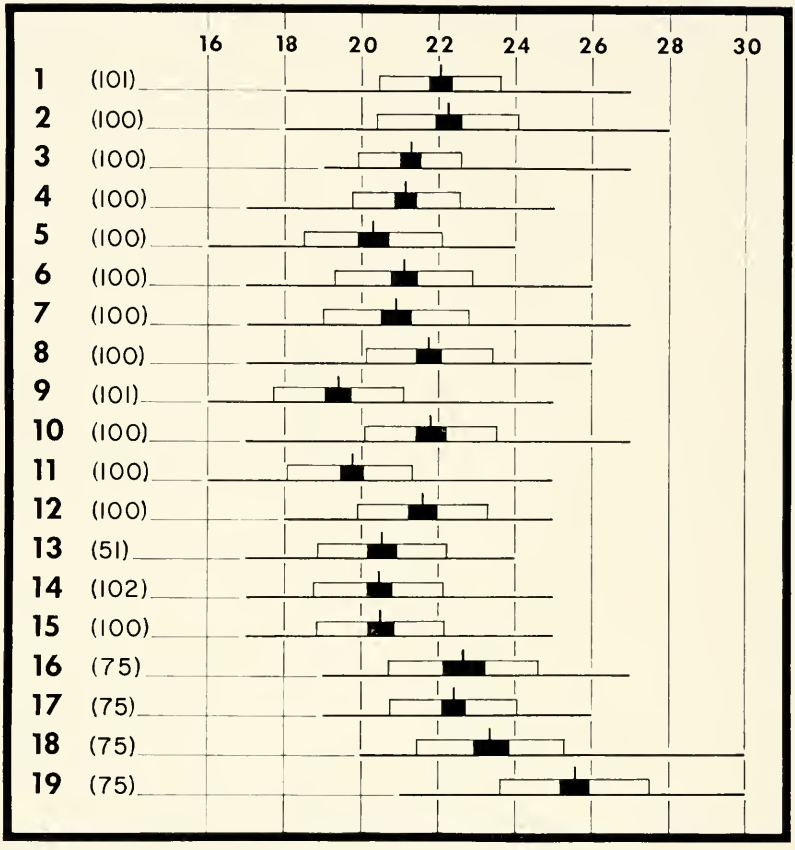


Figure 3. Variation in the number of predorsal scales in *Chirostoma jordani*. For localities and explanation of the diagrams see legends of Figs. 1 and 5.

rango City, hwy. 40; UMMZ 197643 (4), effluent stream below Peñon del Aguila dam, 4.2 mi. N Morcillo, hwy. 45. Guanajuato: USNM 125441, lectotype, USNM 47509 (2), USNM 203104 (1), UMMZ 187660 (1), UMMZ 187661 (1), FMNH 6770 (5), SU 788 (4), CAS 14250 (2), BM 1894 1.27 (7), paralectotypes, Río Lerma and canals at Salamanca; ANSP 90852 (2), USNM 55783 (5), FMNH 3598–3599 (23), Acámbaro; TU 31884 (1), Lake Yuriria, 8.2 mi. around W end of lake from town of Yuriria; UMMZ 197627 (77), **14**, TU 37747 (9126), S shore of Lake Yuriria ca. 1.5 mi. E of Yuriria; USNM 23135 (6), Alberca, Valle de Santiago; UMMZ 197602 (90), **13**, UMMZ 197620 (598), UMMZ 197645 (2), Río Turbio 8 mi. E Pénjamo at hwy. 110 crossing; UMMZ 197603 (23), Solis dam 4 mi. N Acámbaro, UMMZ 197625 (461), ditch draining into W end of Lake Yuriria 2.5 mi. N jct. hwys. 43 and 49; **12**, UMMZ 197621 (386), trib. to Río Turbio 18.5 mi. NW Cuerámaro; UMMZ 197619 (89), trib. to Río Lerma 5 mi. NE Piedad at hwy. 110 crossing. Hidalgo: P 768 (41), Río Tula at Endó dam (Pánuco drainage); **19**, UMMZ 197628 (148), UMMZ 197629 (247), dam 1.1 mi. W jct. hwys. 130 and 119 (to Zacatlán). Jalisco: UMMZ 173567 (ca. 1615), Lake Tilapana (Lake Atotonilco) at town of Tizapanito (Villa Corona); UMMZ 154335 (19), roadside pond 11 mi. SW of Guadalajara; UMMZ 164698 (36), el Canal de la Presa de Logado ca. 12 mi. S of Guadalajara on Jalisco hwy. no. 35—Guadalajara–Chapala; UMMZ 179714 (3), flooded edge of Lake Chapala ca. 1 mi. S of Ocotlán near source of Río Grande de Santiago; UMMZ 108642 (25), Río Grande de Santiago between Ocotlán and Lake Chapala; UMMZ 173561 (41), Lake Colorado sev. mi. E of Etzatlán; UMMZ 173804 (1), Río Ameca, 7 mi. E of Ameca; UMMZ 179744 (1), Lake Chapala at Tuxcueca on S side of lake; UMMZ 179702 (5), lateral irrigation ditch off main E–W canal, 2.5 mi. due N of Etzatlán on road to Magdalena; TU 31956 (25), Río Santiago at Poncitlán; UMMZ 197608 (6), TU 31994 (1), Río Santiago et El Salto de Juanacatlán, below falls; **3**, TU 37761 (633), dam ca. 2 mi. W of Lagos de Moreno on hwy. 80; **4**, TU 37757 (255), dam ca. 7 mi. W Lagos de

Moreno on hwy. 80; TU 37751 (3), Alcala dam on Río San Juan de los Lagos, ca. 2 mi. E San Juan de los Lagos; **5**, TU 37760 (766), trib. to Río Verde ca. 6 mi. NE Valle de Guadalupe on hwy. 80; **6**, TU 37756 (119), trib. to Río Verde 2 mi. NE Valle de Guadalupe on hwy. 80; **9**, TU 37752 (58), Lake Chapala 0.2 mi. E of El Fuerte (E end of lake); **9**, TU 37749 (288), Lake Chapala at source of Río Santiago, 0.5 mi. SW town of Cuitzeo, TU 37759 (26), Río Santiago at Poncitlán; **8**, TU 37758 (819), TU 37750 (242), Lake Atotonilco 0.25 mi. E of Villa Corona; **7**, TU 37748 (1735), Lake Cajititlán at Cajititlán; UMMZ 197609 (1), Río Santiago 3.7 mi. E Atequiza; UMMZ 197607 (36), Lake San Marcos, 8.8 mi. S Acatlán de Juarez, México: UMMZ 197631 (83), small flooded corner of field between San Juan Zitlaltepec and Lake Zumpango. México D.F.: UMMZ 97659 (142), N end of old basin of Lake Texcoco, 2 mi. SE of San Cristobal Exatepec; UMMZ 97660 (53), SW shore of old basin of Lake Texcoco, Valley of Mexico, 9–14 km on Puebla Road; UMMZ 108623 (28), E shore of Lake Texcoco; **17**, UMMZ 173502 (177, additional 71 in exchange coll.), ditch leading into Lake Texcoco, 12 mi. E Mexico City; **16**, TU 37754 (53), canal at W edge of Mixquic; ANSP 90856 (5), FMNH 3685 (13), Xochimilcho. Michoacán: UMMZ 173517 (1306, additional 163 in exchange coll.), Lake Cuitzeo; UMMZ 172189 (31), spring-fed pool on S side of Lake Cuitzeo near causeway; UMMZ 167678 (8), 2 mi. E of La Palma, SE side of Lake Chapala; UMMZ 173627 (16), Lake San Anton (dam at Hauracha) SW of Zamora (not natural lake); UMMZ 173635 (1), canal at Tarecuato (behind dam) SW of Zamora; will form new dam for irrigation; **11**, TU 31923 (288) Wilson dam at La Estancia de Villa Jimenez 14.3 mi. NE Zacapu; **15**, TU 31890 (126), S shore of Lake Cuitzeo at end of causeway, 3.3 mi. S Cuitzeo on hwy. 47; TU 37755 (26), trib. to Río Lerma at NE end of Tanhuato above the bridge; TU 37753 (8), S shore of Lake Cuitzeo along the causeway; USNM 48210 (3), Lake Cuitzeo; UMMZ 197615 (157), trib. to Río Lerma at N end of Tanhuato below earthen dam; **10**, UMMZ 197646 (148), spring-fed pond N Jaripo; UMMZ 197637 (23), irrigation ditch 5.5 mi. NE Alvaro Obregón; UMMZ 197636 (1), irrigation ditch (Río Grande de Morelia?) 3.7 mi. NE Alvaro Obregón; UMMZ 197626 (116), S shore Lake Cuitzeo, E side of causeway around flooded spring. Morelos: USNM 121844 (39), Yautepec, bought in market. Tlaxcala: P 637 (12); Lake Carmen; **18**, UMMZ 197630 (221), effluent from warm spring, S side of hwy. 1 mi. E El Carmen.

CHIROSTOMA PATZCUARO MEEK

Chirostoma patzcuaro Meek, 1902:112, holotype: FMNH 3628, type locality: Lake Pátzcuaro, Michoacán, 1904:174, Fig. 56; Regan, 1906–08:58; Jordan and Hubbs, 1919:73, Fig. 26; Jordan, Evermann and Clark, 1930: 250; Cuesta Terron, 1931:239; Solórzano, 1961:20, Fig. 4; Alvarez and Cortés, 1962: 124; Alvarez, 1970:124. *Chirostoma bartoni* var. *patzcuaro*, De Buen, 1940b:22, 1940c: 49. *Chirostoma regani*, Martin del Campo, 1940:483 (in part). *Chirostoma bartoni*, De Buen, 1941d:73 (in part), 1943:212 (in part). *Chirostoma bartoni bartoni*, De Buen, 1941c:5 (in part), 1942:41 (in part), 1944a: 264 (in part), Schultz, 1948:31 (in part); Alvarez, 1950a:100 (in part). *Eslopsarum bartoni bartoni*, De Buen, 1945:506 (in part), 1946b:114 (in part).

Diagnosis.—Median lateral scales, 52–63; predorsal scales, 24–34; anal rays, 15–18; gill rakers, 23–29; head length, 24.5–25.9 in percent of standard length; eye length, 5.6–6.1; mandible length, 8.8–9.9; length of anal fin base, 16.6–20.6; snout pointed to moderately pointed; scale margins laciniate.

Description.—Maximum length of specimens examined 104 mm S.L.; body slender; head moderate, subtriangular to triangular; snout included by lower jaw; teeth small, in bands, none on vomer or palatines; predorsal scales slightly crowded; lateral line scales with pores and canals; pectoral fins moderately long and pointed.

Range.—Known only from the type locality, Lake Pátzcuaro, Michoacán.

Materials examined.—Michoacán: FMNH 3628, holotype; FMNH 3629 (1), ANSP 90842 (1), paratypes; TU 30882 (6); TU 40852 (16). All from Lake Pátzcuaro.

CHIROSTOMA CHAPALAE JORDAN AND SNYDER

Fig. 17d

Chirostoma chapalae Jordan and Snyder, 1899: 135, holotype: SU 6155, type locality: Ocotlán, Jalisco (Lake Chapala); Jordan and Evermann, 1896–1900:3159; Pellegrin, 1901: 205; Meek, 1902:115, 1904:176, Fig. 58; Regan, 1906–08:61; Jordan and Hubbs, 1919: 76, Fig. 28; Jordan, Evermann and Clark, 1928:251; Cuesta Terron, 1931:239; De Buen, 1940c:49, 1943:212, 1945:515, 1946a:278, 1946b:114; Schultz, 1948:31; Alvarez, 1950: 103, 1970:127; Alvarez and Cortés, 1962:124.

Diagnosis.—Median lateral scales, 44–55; predorsal scales, 29–49; gill rakers, 25–29; head length, 23.8–25.5 in percent of standard length; mandible length 8.6–9.4. Distinguished from *C. consocium consocium* (ranges and means in parentheses) by a smaller maximum size, 87 mm S.L. (125 mm S.L.); having fewer median lateral scales, $\bar{x} = 49.7$ (52–68, $\bar{x} = 60.7$); fewer predorsal scales, $\bar{x} = 37.1$ (43–79, $\bar{x} = 55.6$);

shorter head, $\bar{x}$ = 24.5 (24.4–28.0, $\bar{x}$ = 26.2); shorter mandible, $\bar{x}$ = 8.9 (9.2–11.0, $\bar{x}$ = 10.1); narrower caudal peduncle, 7.6–8.8, $\bar{x}$ = 8.3 (8.2–9.8, $\bar{x}$ = 9.0).

Description.—Body slender; mouth small, oblique, more so than in *C. c. consocium*; jaws weak but project slightly beyond a pointed, angular snout exposing teeth; teeth small, in a narrow band on premaxillaries and in two or three rows or a wider band on the dentaries, none on vomer or palatines; scales deciduous, margins laciniate, but not as strongly so as in the larger species, moderately crowded in predorsal region; lateral line scales with canals; pectorals moderately long and pointed. Melanophores usually found faintly concentrated along the posterior margin of the caudal fin.

Remarks.—Jordan and Hubbs (1919) reported hybrids between *C. chapalae* and *C. consocium*. Their specimens fall within the normal range of overlap between the two species and being small lack adult body proportions. Hybridization between the two forms is not ruled out, but an accurate determination of Jordan and Hubbs' specimens is not possible. A few specimens showing mixed affinities between these two species have been collected from the Río Grande de Santiago at Poncitlán (UMMZ 197612, UMMZ 197613).

Range.—Lake Chapala, Jalisco-Michoacán and the Río Grande de Santiago at Poncitlán. Two collections in the U.S. National Museum of Natural History are labeled "Morelos" and "Puebla." Although records of *C. chapalae* from outside the present Lake Chapala basin would be of great interest, I consider these localities to be in error.

Material examined.—Jalisco: SU 6155, holotype, Lake Chapala at Ocotlán, SU 6209 (6), paratypes, same data as the holotype. UMMZ 108640 (3), Río Grande de Santiago between Ocotlán and Lake Chapala, or outlet end of lake nearby; UMMZ 124463 (127), Lake Chapala; UMMZ 179716 (2), flooded edge of Lake Chapala ca. 1 mi. S of Ocotlán near source of Río Grande de Santiago; UMMZ 173543 (61), Lake Chapala, N shore, 0.5 mi. W town of Chapala at Manglar; TU 40836 (225), Lake Chapala at Ajijic; TU 40813 (1), Lake Chapala 0.2 mi. E El Fuerte, at E end of lake; TU 40873 (1), UMMZ 197612 (22), TU 40822 (1), Río Santiago at Poncitlán; TU 40878 (48), Lake Chapala 4.8 mi. W town of Chapala at Ajijic. Michoacán: UMMZ 187667 (4), La Palma. Morelos: USNM 130898 (1), Morelos? Puebla: USNM 130882 (75), Puebla?

CHIROSTOMA HUMBOLDTIANUM (VALENCIENNES)

Fig. 16b

Atherina humboldtiana Valenciennes, 1835: 479, Pl. 306, holotype: presumably in the Berlin Museum (Maurice Blanc, Paris Museum, pers. comm.), type locality: Valley of Mexico. *Atherina vomerina* Valenciennes, 1835:481. *Atherinichthys humboldtii*, Gunther, 1861:404. *Atherina fontinalis* Châzari, 1884:80. *Chirostoma humboldtianum*, Von Bayern and Steindachner, 1895:522, Pl. 1, Fig. 1; Jordan and Evermann, 1895:330, 1896–1900:793; Evermann, 1893:103; Jordan and Snyder, 1899: 134; Evermann and Goldborough, 1901:152; Meek, 1902:114 (in part), 1904:175 (in part); Regan, 1906–08:60; Jordan and Hubbs, 1919:73, Fig. 27; Jordan, Evermann and Clark, 1928:250; Cuesta Terron, 1931:239; Altini, 1940:104; Martin del Campo, 1940:484; De Buen, 1940b:24, 1940c:49, 1942:42, 1943:212, 1945:512, 1946b:114; Schultz, 1948:31; Alvarez, 1950a: 103, 1970:127; Alvarez and Navarro, 1957: 40; Romero, 1967:69. *Chirostoma humboldtiana*, Seurat, 1898:26. *Chirostoma regani*, Jordan and Hubbs, 1919:74; Jordan, Evermann and Clark, 1928:250; Martin del Campo, 1940:485 (in part); De Buen, 1940c: 49, 1941b:5; Schultz, 1948:31; Alvarez, 1950: 100, 1970:124; Alvarez and Navarro, 1957: 46. *Chirostoma bartoni*, De Buen, 1943:214 (in part); Solórzano, 1961:15 (in part). *Chirostoma bartoni bartoni*, De Buen, 1941c: 7 (in part), 1942:41 (in part), 1944a:269 (in part); Alvarez and Cortés, 1962:123 (in part). *Chirostoma breve*, Regan, 1906–08: 59, Pl. 10, Fig. 3 (in part); Altini, 1940:103 (in part). *Eslopsarum regani*, De Buen, 1945:509, 1946b:114. *Chirostoma ocampoi* Alvarez, 1963a:197, 1970:126.

Diagnosis.—Median lateral scales, 43–73; predorsal scales, 24–50; gill rakers, 19–28; distance from snout to pelvic fin origin, 40.9–51.2 in percent of standard length; head length, 25.6–34.2; postorbital head length, 12.2–16.8; eye length, 4.6–7.8; snout length, 8.4–13.4; length of anal fin base, 17.1–22.2.

Description.—Maximum length for species approximately 200–250 mm S.L.; body slender to moderately deep; snout blunt or subtriangular, equal to or included by a slightly projecting lower jaw; teeth small, in bands, two or three occasionally present on vomer; scale margins laciniate lateral line scales with canals; predorsal scales moderately crowded; pectoral fins short, slightly pointed.

Remarks.—The reported presence of *C. humboldtianum* in Lake Pátzcuaro and of

C. estor in the Valley of Mexico by Meek (1902, 1904) has been a steady source of confusion. Alvarez and Navarro (1957) suggest that he either bought them in a market and was given erroneous locality data or that he mixed his collections accidentally. The latter interpretation seems to be the most reasonable. There can be little doubt, however, about the former presence of the nominal *C. regani* in Lake Pátzcuaro although it has not been taken there since Meek's time. Jordan and Hubbs removed the type series for this species (FMNH 73321) from the type series of *C. patzcuaro*. One specimen, possibly a hybrid between the two species, still remains with the paratypes, FMNH 3629.

The morphological differences separating *C. regani* from *C. humboldtianum* noted by Jordan and Hubbs (1919) disappear when specimens of the same size are compared leaving only differences in length and number of median lateral and predorsal scales as diagnostic characters. Length is easily affected by environmental conditions. The two scale characters have too much overlap to justify taxonomic recognition even at the subspecific level. Perhaps *C. regani* represents a form close to *C. patzcuaro* and *C. humboldtianum* once present in the upper Lerma basin but which has introgressed with both species. The capture of a fish in Lake Zacapu, Michoacán identical to the local population of *C. humboldtianum* except for its slightly smaller size and larger scales (median lateral scales, 43; predorsal scales, 20), is significant in this regard.

Chirostoma ocampoi Alvarez described from Lake Zacapu is herein synonymized with *C. humboldtianum*. Although this nominate form has a slightly higher number of gill rakers, taxonomic recognition at any level is not warranted.

The three western populations of *C. humboldtianum* differ from their eastern counterparts by having higher mean values for median lateral and predorsal scales. Overlap is too great, however, to justify a subspecific name. These forms are in danger of extinction. Largemouth bass were introduced into the lake north of Santa Maria in 1961 and into the lake at San Pedro Lagunillas in 1967. All of the poeciliids and goodeids formerly present in the lakes have disappeared. The atherinids have either disappeared (Santa Maria) or have been reduced to an extremely low population level (San Pedro Lagunillas). Lake Juanacatlán, near Navidad, Jalisco, the most remote, was free from introductions in 1963. *C. humboldtianum* is the only fish species at this locality.

The population formerly inhabiting Lake Santa Maria was unusual in possessing a slightly lower number of vertebrae. This was perhaps due to the higher temperature of the water in which they lived.

Specimens of uncertain status.—SU 48299. Three specimens in very poor condition labeled "*Chirostoma humboldtianum* Pátzcuaro." The number of rakers on the first arch, 25, 28, and 28, preclude their being *C. humboldtianum* and an estimated 61, 61, and 63 median lateral scales is slightly low for *C. estor estor*. Strongly projecting lower jaws suggest that they are *C. lucius* from Lake Chapala.

Range.—Lakes within the Valley of Mexico, Río Lerma at Tepuxtepec, Michoacán, Lake Zacapu at Zacapu, Mich., Lake Santa Maria, Santa Maria, Nayarit, Lake at San Pedro Lagunillas, Nay., Lake Juanacatlán, about 10 miles west of Navidad, Jalisco (Fig. 4). See Alvarez and Navarro (1957) for Valley of Mexico localities.

Material examined.—Jalisco: TU 40825 (756) isolated lake about 5 mi. W of Navidad, E of Mascota; USNM 126979 (2), USNM 48839 (3), La Laguna, Sierra de Juanacatlán. México, D. F.: USNM 30485 (3), ANSP 27061–72, City of Mexico; ANSP 14609–13 (6), Lake Chalco; USNM 55785 (6), USNM 55852 (2), UMMZ 187663 (2), UMMZ 187672 (5), UMMZ 187673 (1), FMNH 73320 (109), Xochimilcho; SU 9413 (3), canals, Chalco; SU 9407 (5), Xochimilcho; SU 31945 (3), Valley of Mexico; SU 6210 (28), Mexico City market (said to be from Lake Chalco); SU 17171 (16), Lake Chalco (market, city of Mexico); UMMZ 97662 (1), SW shore of old basin of Lago de Texcoco; UMMZ 97663 (10), Mexico City fish market, vicinity of Xochimilcho, Valley of Mexico; UMMZ 132732 (1), alkaline lake (perhaps Lake Chimalhuacán) Lake Texcoco? Mexico?; FMNH 3687, holotype of *C. regani*, Xochimilcho; FMNH 59536 (10), paratypes of *C. regani*, Xochimilcho; FMNH 43153 (3), paratypes, *C. regani*, Xochimilcho; P 641 (5), P 461 (5), P 810 (4), Chimalhuacán; USNM 51010 (6), Mexico City market, said to have come from Texcoco; UMMZ 187662 (3), USNM 55786 (3), Chalco. Michoacán: USNM 197516 (2), paratypes of *Chirostoma ocampoi*, Laguna de Zacapu; USNM 45534 (3), Michoacán (Pátzcuaro?); UMMZ 197635 (1027),

behind Tepuxtepec dam at Tepuxtepec; UMMZ 197639 (4), outlet stream from Lake Zacapu at Zacapu; TU 40850 (13), TU 31933 (58), Lake Zacapu at Zacapu, mostly in outlet stream; TU 40867 (22), Lake Zacapu at Zacapu; FMNH 73321 (4), Pátzcuaro. NAYARIT: FCB 106 (4), TU 40826 (658), Lake just E of San Pedro Lagunillas, about 13 mi. E of Compostela; UMMZ 178317 (319), TU 40828 (10), Lake Santa Maria, about 27 mi. SE of Tepic.

Specimens of unknown localities.—USNM 37804 (2), USNM 39408 (3), USNM 37791 (1).

CHIROSTOMA CONSOCIUM CONSOCIUM JORDAN AND HUBBS

Fig. 17c

Chirostoma consocium Jordan and Hubbs, 1919: 76, holotype: FMNH 3672, type locality: Lake Chapala at La Palma, Michoacán; Jordan, Evermann and Clark, 1928:251; De Buen, 1940c:50, 1943:212, 1945:517, 1946a: 278, 1946b:114; Schultz, 1948:31; Alvarez, 1950a:103, 1970:127; Alvarez and Cortés, 1962:125. *Chirostoma grandocule*, Meek, 1902:115 (in part), 1904:176 (in part). *Chirostoma grandoculis*, Regan, 1906–08:61 (in part).

Diagnosis.—Median lateral scales, 52–68; predorsal scales, 43–79; gill rakers, 24–29; distance from snout to second dorsal fin origin, 63.4–66.7 in percent of standard length; distance from snout to origin of pelvic fin, 37.7–43.0; head length, 24.4–28.0; snout length, 7.2–9.5; least depth of caudal peduncle, 8.2–9.8; snout included by a slightly projecting lower jaw; teeth small.

Description.—Largest specimen examined 125 mm S.L.; body slender, to relatively deep in adults, snout pointed; teeth in bands, outer mandibular and inner median premaxillary series enlarged, none on vomer or palatines; scale margins laciniate; predorsal scales crowded; lateral line scales with canals; pectoral fins long and pointed.

Remarks.—On April 1, 1964 *C. c. consocium* was apparently spawning in very shallow water on the north shore of Lake Chapala 1.6 miles west of the town of Chapala. The eggs were attached to small pebbles and stones by threads and were washed up along the shore in small windrows. In this area the males were bronze colored dorsally while the females were more silvery. Unfortunately, turbid water and near darkness precluded observations of breeding behavior.

Range.—Lake Chapala, Jalisco–Michoacán and the Río Grande de Santiago at Poncitlán (Fig. 4).

Material examined.—JALISCO: UMMZ 179718 (3), flooded edge of Lake Chapala ca. 1 mi. S of Ocotlán, near source of Río Santiago; UMMZ 108637 (3), Río Grande de Santiago between Ocotlán and Lake Chapala or outlet of lake nearby; UMMZ 179720 (6), Lake Chapala at Jamay near E end of lake; UMMZ 179748 (2), Lake Chapala at Texcueca on S side of lake; UMMZ 197613 (4), TU 40819 (23), TU 31957 (13), Río Santiago at Poncitlán; TU 31969 (233), Lake Chapala 1.6 mi. W town of Chapala; TU 31927 (3), Lake Chapala 15.8 mi. W of town of Chapala at Jocotepec; TU 31989 (400), Lake Chapala at Ajijic; TU 40815 (11), Lake Chapala ca. 0.2 mi. E of El Fuerte at E end of lake; TU 40832 (3), Lake Chapala at Ajijic by cement pier; TU 40833 (2), Lake Chapala, Isla de los Alacranes, S shore in areas especially cleared for throw-net by fisherman; TU 40845 (5,000+), Lake Chapala at Ajijic. MICHOACÁN: FMNH 3672, holotype; SU 17776 (6), paratypes; UMMZ 187668 (6), all from La Palma.

CHIROSTOMA CONSOCIUM RESERATUM ALVAREZ

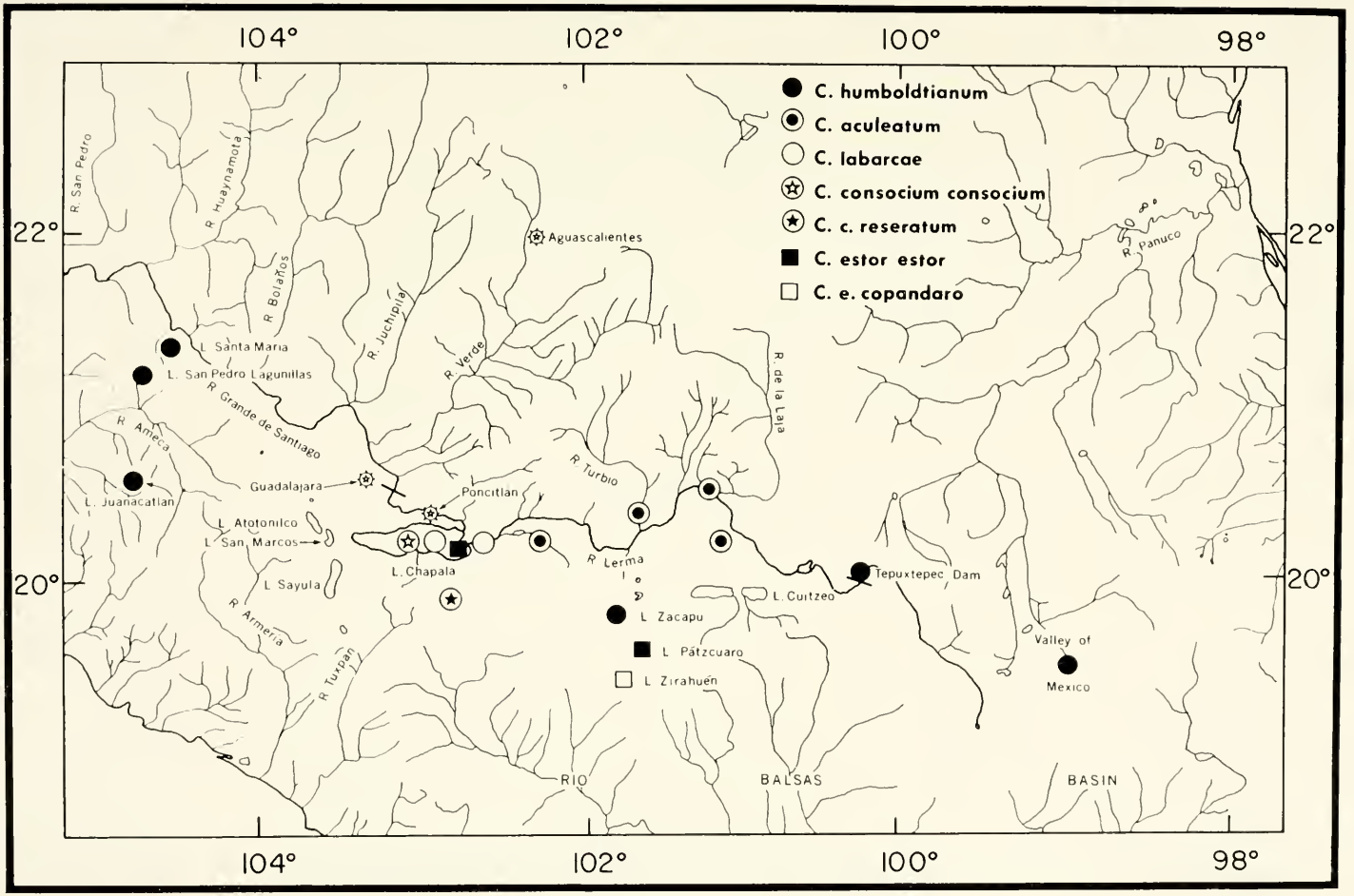
Fig. 18c

Chirostoma reseratum Alvarez, 1963b:130, holotype: P732, type locality: San Juanico dam, near Cotija, Michoacán, 1970:128.

Diagnosis.—Differs from the nominate form (ranges and means in parentheses) by having fewer predorsal scales, 33–56, $\bar{x}$ = 42.4 (43–79, $\bar{x}$ = 55.6); fewer anal fin rays, 16–21, $\bar{x}$ = 18.2 (17–24, $\bar{x}$ = 20.3); shorter anal fin base, 20.2–23.2, $\bar{x}$ = 21.4 (21.7–26.2, $\bar{x}$ = 23.9). Differs from *C. humboldtianum* by having a higher number of gill rakers, 23–30, $\bar{x}$ = 27.2 (19–28, $\bar{x}$ = 23.0); shorter distance from snout to pelvic fin origin, 39.7–43.3, $\bar{x}$ =41.0 (40.9–51.2, $\bar{x}$ = 44.0) in percent of standard length; shorter postorbital head length, 11.5–13.2, $\bar{x}$ = 12.3 (12.2–16.8, $\bar{x}$ = 13.8); longer eye, 6.2–7.4,

→

Figure 4. Distribution of five species and two subspecies of *Chirostoma* on the Mesa Central of Mexico. For explanation of figure see legend of Fig. 1.


104°
102°
100°
98°
22°
20°
C. humboldtianum
C. aculeatum
C. labarcae
C. consocium consocium
C. c. reseratum
C. estor estor
C. e. copandaro
R. San Pedro
R. Huaynamota
R. Bolaños
R. Juchipila
R. Verde
Aguascalientes
R. Panuco
L. Santa Maria
L. San Pedro Lagunillas
R. Grande de Santiago
R. Ameca
L. Juanacatlan
Guadalajara
Poncitlan
L. Atotonilco
L. San Marcos
L. Sayula
L. Chapala
R. Armeria
R. Turbio
R. Lerma
R. de la Laja
L. Zacapu
L. Pátzcuaro
L. Zirahuén
L. Cuitzeo
Tepuxtepec Dam
Valley of
Mexico
R. Turxpan
RIO
BALSAS
BASIN

$\bar{x}$ = 6.9 (4.6–7.8, $\bar{x}$ = 5.9); shorter snout, 7.5–9.5, $\bar{x}$ = 8.6 (8.4–13.6, $\bar{x}$ = 10.0); longer anal fin base, (17.1–22.2, $\bar{x}$ = 19.4). Differs from all other species of *Chirostoma* in the following characters: median lateral scales, 56–69; number of predorsal scales and gill rakers; distance from snout to origin of first dorsal fin, 49.0–51.7; head length, 25.9–28.2; eye length; mandible length, 9.8–11.2; second dorsal fin height, 14.9–18.7; anal fin height, 15.7–18.6.

Description.—Largest specimen examined 114 mm S.L. (218 mm S.L., Alvarez, 1963); body slender; head triangular; snout moderate, included by lower jaw; teeth small, in bands, outer members on dentaries and on median portions of the premaxillaries enlarged, none on vomer or palatines; scale margins laciniate; predorsal scales crowded; lateral line scales with canals; pectoral fins long and pointed.

Remarks.—Morphologically, the nominal *C. reseratum* overlaps both *C. consocium* and *C. humboldtianum* to the extent that recognition at the specific level is not warranted. No differences or apparent patterns emerge when the following characters are compared: distances from snout to first and second dorsal fin origins, length and least depth of caudal peduncle, greatest depth, length of mandible and second dorsal base and interorbital distance. *C. reseratum* falls more or less in between the two species in the number of anal fin rays and in the length of the anal fin base, head, pectoral and pelvic fins. *C. reseratum* and *C. consocium* show varying degrees of concordance when the following characters are examined: number of median lateral scales and gill rakers, height of second dorsal and anal fins, eye width, distances from snout to origin of pelvic and anal fins and snout and postorbital head lengths. Because of the agreement in these characters, *C. reseratum* is treated as a subspecies of *C. consocium.*

Range.—San Juanico dam and effluent stream near Cotija, Michoacán (Fig. 4).

Material examined.—Michoacán: P732 (10), paratypes, TU 40865 (134), TU 31946 (56), San Juanico dam 5 mi. SE Cotija; UMMZ 197642 (3), effluent channel below San Juanico dam 5 mi. SE Cotija.

CHIROSTOMA GRANDOCULE (STEINDACHNER)

Atherinichthys grandoculis Steindachner, 1894: 149, holotype: apparently lost in the collection of the Naturhistorisches Museum, Vienna, type locality: Lake Pátzcuaro, Michoacán. *Chirostoma grandocule*, Von Bayern and Steindachner, 1895:525, Pl. 2, Fig. 1; Jordan and Evermann, 1895:330, 1896–1900:2839; Meek, 1902:115 (in part), 1904:176 (in part); Jordan and Hubbs, 1919:79; Jordan, Evermann and Clark, 1928:251; Cuesta Terron, 1931:239; De Buen, 1940a:307, 1940c: 50, 1941d:74 (in part), 1943:212 (in part), 1945:516, 1946b:114; Martin del Campo, 1940:483; Schultz, 1948:31; Alvarez, 1950a: 102, 1970:126; Alvarez and Cortés, 1962:124.

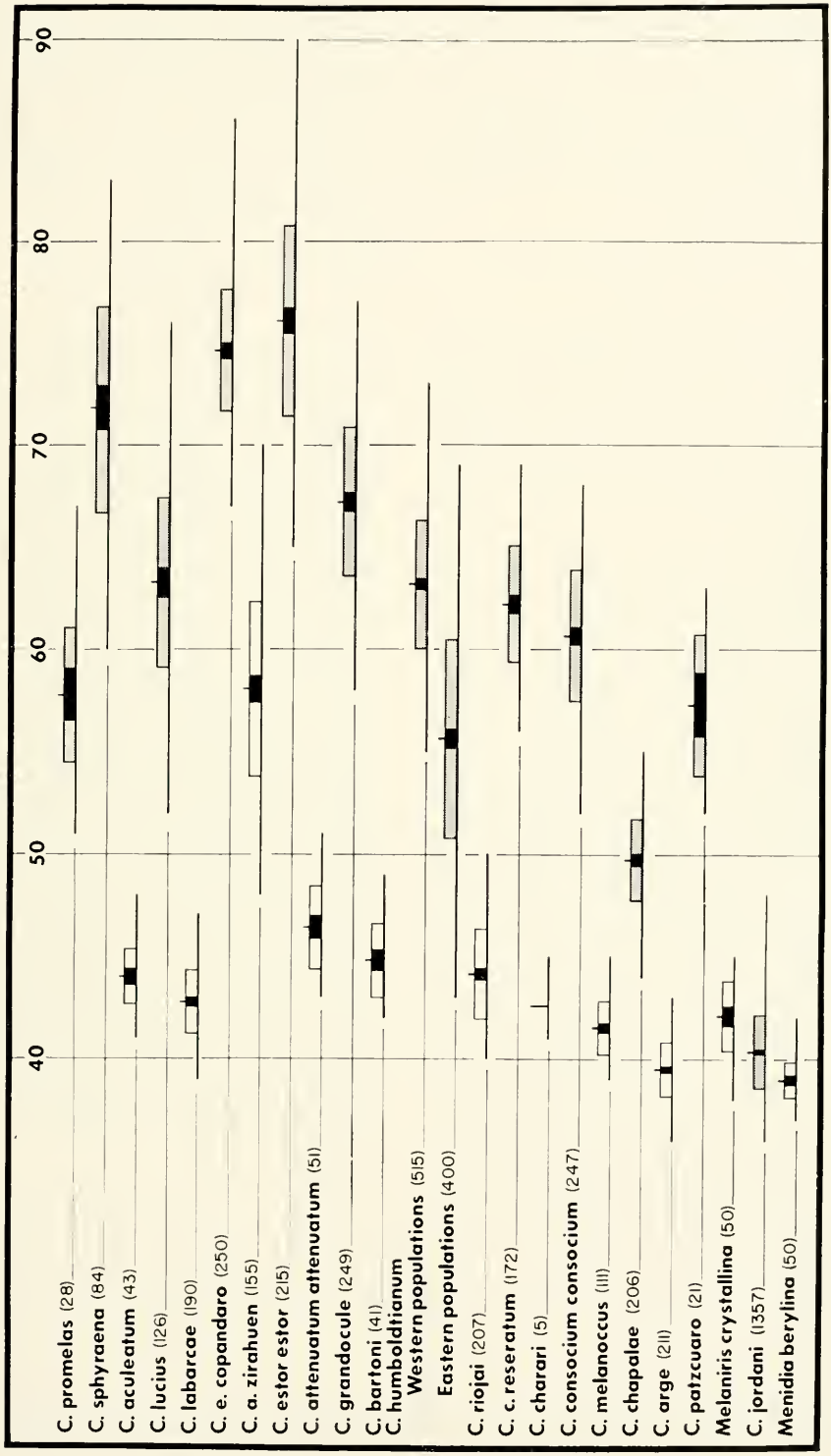
Diagnosis.—Median lateral scales, 58–77; gill rakers, 28–34; anal rays, 18–22; least depth of caudal peduncle, 7.3–8.1 in percent of standard length; height of second dorsal fin, 13.3–14.8; height of anal fin, 13.8–16.2.

Description.—Largest specimen examined 170 mm S.L.; body slender; mouth small; snout short and blunt in adults, included by lower jaw; teeth small, in bands, none on vomer or palatines; predorsal scales moderately crowded; scale margins laciniate; lateral line scales with canals and pores; pectoral fins moderate, slightly pointed.

Remarks.—This species has an exceptionally high number of gill rakers.

→

Figure 5. Comparison of the number of median lateral scales in *Menidia berylina, Melaniris crystallina* and *Chirostoma.* The diagrams indicate the mean (center point), 95 percent confidence limits of the mean (black rectangle), one standard deviation on either side of the mean (outer limits of open rectangle) and sample range (base line). The sample size is given in parentheses following the species name or locality. The sequence of the species is, for the most part, based on presumed phylogenetic relationships with the most primitive at the bottom and the most specialized at the top of the figure. Western populations of *C. humboldtianum* refer to specimens from Lakes Juanacatlán (Navidad), San Pedro Lagunillas and Santa Maria; eastern populations refer to the Tepuxtepec dam, Lake Zacapu and the Valley of Mexico (Fig. 4). Stippling within the standard deviation rectangle denotes members of the jordani species group; clear rectangles denote the arge species group and the possible persistent ancestors of *Chirostoma, Menidia berylina* and *Melaniris crystallina.*


40
50
60
70
80
90
C. promelas (28)
C. sphyraena (84)
C. aculeatum (43)
C. lucius (126)
C. labarcae (190)
C. e. copandaro (250)
C. a. zirahuen (155)
C. estor estor (215)
C. attenuatum attenuatum (51)
C. grandocule (249)
C. bartoni (41)
C. humboldtianum
Western populations (515)
Eastern populations (400)
C. riojai (207)
C. c. reseratum (172)
C. charari (5)
C. consocium consocium (247)
C. melanoccus (111)
C. chapalae (206)
C. arge (211)
C. patzcuaro (21)
Melaniris crystallina (50)
C. jordani (1357)
Menidia berylina (50)

Range.—Known only from the type locality, Lake Pátzcuaro, Michoacán.

Material examined.—Michoacán: TU 40854 (1577), Lake Pátzcuaro, W of Ihuatzio; TU 40861 (4), TU 40880 (14), Lake Pátzcuaro between Napizaro, Jacuaro and Erongaricuaro; TU 40857 (557), Lake Pátzcuaro, S shore of Isla de Yuñen; USNM 55784 (4), UMMZ 187665 (3), Pátzcuaro.

CHIROSTOMA COMPRESSUM DE BUEN

Chirostoma grandocule compressum De Buen, 1940a:306, holotype: lost, originally deposited in the collection of the Pátzcuaro Limnological Station, type locality: Lake Cuitzeo, Michoacán, 1941c:7, 1943:213, 1944a:268. *Chirostoma grandocule,* De Buen, 1941d:74 (in part). *Chirostoma compressum,* De Buen, 1945:518, 1946b:114; Schultz, 1948:31; Alvarez, 1950a:103, 1970:126; Alvarez and Cortés, 1962:125.

Description.—De Buen seems to be the only ichthyologist who has seen this species. His most extensive description (1945), translated, is presented below.

"Body long, compressed; greatest depth and width 72–82 and 42–50 percent of head, respectively; head 19–21 percent of total length; mouth small, weakly oblique, protractile; lower jaw slightly projecting; chin pointed and delicate; orbit 26–30, preorbital distance 33–37.5 and postorbital distance 26–30 percent of head; scales crenulate, 64–67 in the lateral line, 15–16 in the transverse series; teeth small, embedded; 30 long and delicate rakers on the first arch, 23 on the descending portion; first dorsal I, 5–6, origin above insertion of pelvics, midway between tip of snout and base of caudal; second dorsal I, 11–12; anal I, 20–22, inserted in advance of and extending a little behind the second dorsal; color pale, lateral stripe extending along the flanks; dorsal part of head dark; fins pale, second dorsal and caudal slightly darkened; membrane surrounding the ovaries jet black; internal face of the peritoneum is, in part, silver; lengths of two specimens 86 and 101 mm."

Remarks.—*C. compressum* seems to be very close to *C. grandocule.* The species has not been seen since De Buen first collected it and is thought to be extinct. The drying of Lake Cuitzeo during the winter of 1941 (De Buen, 1943) no doubt contributed to its presumed demise. Whereas *C. jordani* was able to survive in small springs and tributaries, a larger species would, perhaps, have difficulty doing so.

Range.—Known only from the type locality, Lake Cuitzeo, Michoacán.

Material examined.—None.

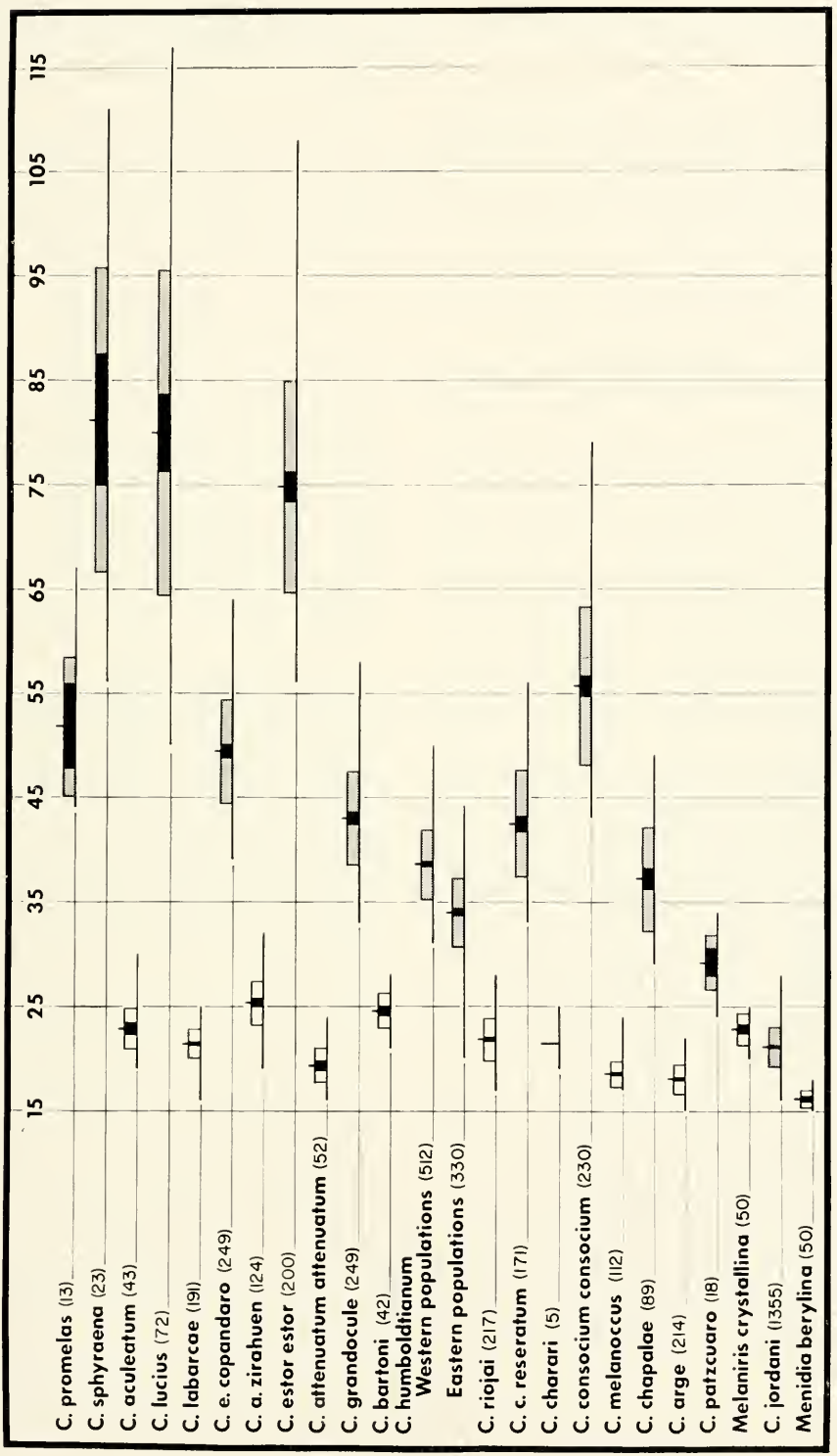
CHIROSTOMA ESTOR ESTOR JORDAN

Chirostoma estor Jordan, 1879:298, holotype: USNM 23124, type locality: Lake Chapala; Von Bayern and Steindachner, 1894:166; 1895:523, Pl. 1, Fig. 3; Jordan and Evermann, 1895:21; Jordan and Snyder, 1899: 141; Jordan and Evermann, 1896–1900:2839, 3165; Jordan, 1900:523; Meek, 1902:116 (in part), 1904:180; Regan, 1906–08:60 in part); Jordan and Hubbs, 1919:81 (in part); Jordan, Evermann and Clark, 1928:251 (in part); Cuesta Terron, 1931:241; Martin del Campo, 1940:485; Altini, 1940:104; De Buen, 1940b:10, Fig. 1, 1940c:51, 1940d:3, 1941d: 75, 1943:212 (in part); Alvarez and Navarro, 1957:48; Solórzano, 1963:1–15. *Chirostoma estor* var. *pacanda* De Buen, 1940a:306, 1940b:12. *Chirostoma estor pacanda,* De Buen, 1941a:30, 1941c:8, 1943:215, 1944a: 265, 1945:523, 1946b:115; Schultz, 1948:31; Alvarez, 1950a:104; Alvarez and Cortés, 1962: 126. *Chirostoma estor* var. *tecuena* De Buen, 1940a:306, 1940b:13, 1940d:5. *Chirostoma estor tecuena,* Martin del Campo, 1940:483. *Chirostoma estor estor,* De Buen, 1941a:30, 1941c:8, 1944a:265, 1945:522, 1946b:115; Schultz, 1948:31; Alvarez, 1950a:104, 1970: 124; Alvarez and Cortés, 1962:126. *Lethostole estor,* Jordan and Evermann, 1896–1900: 792. *Atherinichthys albus* Steindachner, 1894: 148. *Chirostoma* (*Atherinichthys*) *albus,* Von Bayern and Steindachner, 1894:165. *Chirostoma album,* Jordan and Snyder, 1899:146; Jordan and Evermann, 1896–1900:3165. *Chirostoma michoacanae* De Buen, 1940a: 306, 1940b:14, Fig. 20, 1940c:51, 1943:212, 1944a:265; Martin del Campo, 1940:483. *Chirostoma grandocule,* De Buen, 1940b:16, 1945:516.

Diagnosis.—Predorsal scales, 56–108; gill rakers, 23–28; snout to origin of second dorsal fin, 64.1–67.8 in percent of standard length; snout to origin of pelvic fin, 44.1–51.3; postorbital head length, 13.6–16.2;

→

Figure 6. Comparison of the number of predorsal scales in *Menidia beryllina, Melaniris crystallina* and *Chirostoma.* See legend of Fig. 5 for explanation of the diagrams.


15
25
35
45
55
65
75
85
95
105
115
C. promelas (13)
C. sphyraena (23)
C. aculeatum (43)
C. lucius (72)
C. labarcae (191)
C. e. copandaro (249)
C. a. zirahuen (124)
C. estor estor (200)
C. attenuatum attenuatum (52)
C. grandocule (249)
C. bartoni (42)
C. humboldtianum
Western populations (512)
Eastern populations (330)
C. riojai (217)
C. c. reseratum (171)
C. charari (5)
C. consocium consocium (230)
C. melanoccus (112)
C. chapalae (89)
C. arge (214)
C. patzcuaro (18)
Melaniris crystallina (50)
C. jordani (1355)
Menidia berylina (50)

snout length, 10.5–12.3; least depth of caudal peduncle, 7.3–8.2; length of anal fin base, 16.1–21.0

Description.—Largest specimen examined 273 mm S.L.; head large, triangular; lower jaw projects slightly beyond snout exposing small teeth on anterior portion of mandibles; snout never sharply pointed; gape wide; two or three fang-like teeth occasionally on vomer, none on palatines. Predorsal scales crowded; scale margins laciniate; lateral line scales with canals; pectoral fins small to moderate, rounded or slightly pointed.

Remarks.—Chirostoma estor was described from a specimen received from A. Dugès, a resident of the city of Guanajuato. Dugès presumably bought the fish in the market of that city, obtaining locality information from the vendor. In the catalogue of the U. S. National Museum of Natural History "Guanajuato" is crossed out as the locality and "L. Chapala" written in with the remark: *"Poisson Blanc de Chapala' tel quon l 'apporte a Guanajuato."* As Guanajuato is almost equidistant from Lakes Chapala and Pátzcuaro, it seems reasonable that fishes from both localities were sold there and that the holotype actually came from the latter lake where the species is abundant. However, Meek and Lutz collected seven specimens of *C. estor* from Lake Chapala at La Palma in 1901. As there is a chance that Dugès information was correct, the type locality is retained. To my knowledge, *C. estor* has not been taken from Lake Chapala since 1901.

Meek and Lutz's specimens, FMNH 3672 (1) and SU 17776 (6), labeled "type" and "paratypes" respectively, presumably by Jordan and Hubbs, have no type status.

The food habits and biology of *C. estor estor* have been investigated by De Buen (1944) and Solórzano (1963).

Range.—Known with certainty only from Lake Pátzcuaro, Michoacán and the eastern end of Lake Chapala, Jalisco–Michoacán.

Material examined.—Jalisco: USNM 23124, holotype, Lake Chapala; USNM 44166 (6), Lake Chapala? Michoacán: SU 17776 (6), FMNH 3672 (1), Lake Chapala at La Palma; TU 40855 (21); Lake Pátzcuaro W of Ihuatzio; TU 40863 (90), TU 40886 (135); Lake Pátzcuaro between Napizaro, Jacuaro and Erongaricuaro. UMMZ 187666 (1); Pátzcuaro; USNM 203146 (9); Lake Pátzcuaro.

Specimens of uncertain status.—UMMZ 180082. Two specimens in very poor condition collected by Hobart M. Smith at El Sabeno, near Uruapan, Michoacán during the summer of 1936. In all probability these specimens are close to or conspecific with *C. estor.*

CHIROSTOMA ESTOR COPANDARO DE BUEN

Chirostoma estor copandaro De Buen, 1945:524, holotype: lost, originally deposited in the collection of the Pátzcuaro Limnological Station, type locality: Lake Zirahuén, Michoacán, 1946b:115; Schultz, 1948:31; Alvarez, 1950a:104; Alvarez and Cortés, 1962:127. *Chirostoma estor*, Meek, 1902:116 (in part); Regan, 1906–08:60 (in part); Jordan and Hubbs, 1919:81 (in part); Jordan, Evermann and Clark, 1928:251 (in part); De Buen, 1943:212; *Chirostoma estor pacanda*, Alvarez, 1970:124.

Diagnosis.—Differs from the nominate form (ranges and means in parentheses) by having fewer predorsal scales, 39–64, $\bar{x}$ = 49.3 (56–108, $\bar{x}$ = 74.7); shorter head, 27.3–29.4, $\bar{x}$ = 20.0 (28.0–31.8, $\bar{x}$ = 30.2) in percent of standard length; shorter snout, 9.6–11.4, $\bar{x}$ = 10.2 (10.5–12.3, $\bar{x}$ = 11.4); shorter mandible, 10.3–12.2, $\bar{x}$ = 11.4 (12.2–14.8, $\bar{x}$ = 13.2). Differs from *C. humboldtianum* by having a greater number of median lateral scales, 67–86, $\bar{x}$ = 74.6 (43–73, $\bar{x}$ = 59.7) and a greater number of predorsal scales (24–50, $\bar{x}$ = 36.2). Differs from all other species in the following characters: number of median lateral and predorsal scales; gill rakers, 23–28; snout length; least depth caudal peduncle, 6.6–7.7.

Description.—Similar to *C. estor estor* except that teeth are apparently absent from the vomer of this subspecies.

Range.—Known with certainty only from the type locality, Lake Zirahuén, Michoacán.

Material examined.—Michoacán: USNM 55787 (4), UMMZ 187664 (4), UMMZ 197650 (300), TU 31919 (447), Lake Zirahuén, 19 mi. S of Pátzcuaro.

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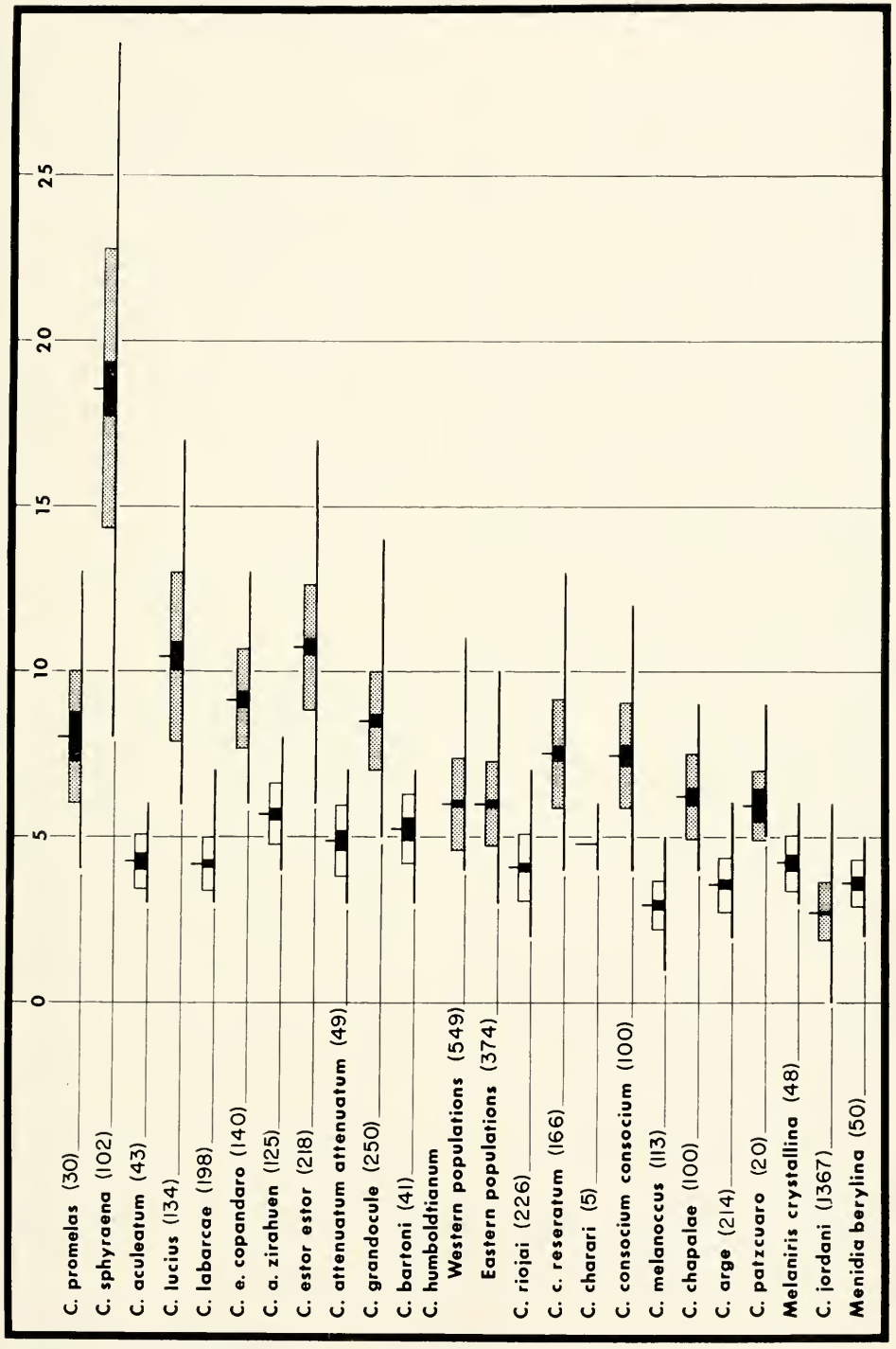
Figure 7. Comparison of the number of interdorsal scales in *Menidia berylina, Melaniris crystallina* and *Chirostoma.* See legend of Fig. 5 for explanation of the diagrams.


0
5
10
15
20
25
C. promelas (30)
C. sphyraena (102)
C. aculeatum (43)
C. lucius (134)
C. labarcae (198)
C. e. copandaro (140)
C. a. zirahuen (125)
C. estor estor (218)
C. attenuatum attenuatum (49)
C. grandocule (250)
C. bartoni (41)
C. humboldtianum
Western populations (549)
Eastern populations (374)
C. riojai (226)
C. c. reseratum (166)
C. charari (5)
C. consocium consocium (100)
C. melanoccus (113)
C. chapalae (100)
C. arge (214)
C. patzcuaro (20)
Melaniris crystallina (48)
C. jordani (1367)
Menidia berylina (50)

CHIROSTOMA LUCIUS BOULENGER
Fig. 17a

Chirostoma lucius Boulenger, 1900:54 (in part, following Regan), holotype: BM 1892.2.8.75, type locality: Lake Chapala; Jordan and Snyder, 1899:137; Evermann and Goldsborough, 1901:152; Meek, 1902:115, 1904: 178, Fig. 60; Regan, 1906–08: 62; Jordan and Hubbs, 1919:79, Fig. 31; Jordan, Evermann and Clark, 1928:251; Cuesta Terron, 1931:240; De Buen, 1940c:50, 1943:212, 1945:519, 1946a:278, 1946b:115; Schultz, 1948:31; Alvarez, 1950a:104, 1970:128; Alvarez and Cortés, 1962:125. *Chirostoma ocotlanae*, Jordan and Snyder, 1899:19; Jordan and Evermann, 1896–1900:3136; Pellegrin, 1901:205; Meek, 1902:116, 1904:180, Fig. 6; Regan, 1906–08:62, Tab. IX, Fig. 1; Jordan and Hubbs, 1919:80, Figs. 33, 34; Jordan, Evermann and Clark, 1928:251; Cuesta Terron, 1931:241; De Buen, 1940c: 51, 1943:212, 1945:520, 1946a:278, 1946b: 115; Schultz, 1948:31; Alvarez, 1950:104, 1970:128; Alvarez and Cortés, 1962:126. *Chirostoma crystallinum* Jordan and Snyder, 1899:139; Jordan and Evermann, 1896–1900: 3162.

Diagnosis.—Predorsal scales, 50–117; interdorsal scales, 6–17; snout length, 10.5–12.5 in percent of standard length; mandible length, 13.1–17.9; least depth caudal peduncle, 8.3–9.2; snout included by lower jaw whose projection beyond the snout may equal approximately one-half the interorbital distance; teeth small to very large, usually the former.

Description.—Maximum length about 300 mm S.L.; body depth moderate, becoming relatively deep in adults; head and gape large, teeth small and in bands, none on vomer or palatines; scale margins laciniate; predorsal scales crowded; lateral line scales with canals; pectoral fins moderate, pointed.

Remarks.—*C. lucius* and *C. ocotlanae* are herein synonymized; there are no known characters which will separate them. The most conspicuous feature of the nominal *C. ocotlanae*, the greatly protruding lower jaw, is extremely variable and thus useless taxonomically.

Range.—Lake Chapala, Jalisco–Michoacán, and the Río Grande de Santiago at Poncitlán, Jalisco. I consider the locality "Colima," USNM 203147, to be an error. If this specimen was bought in a market it probably came from Lake Chapala.

Material examined.—Colima: USNM 203147 (1), Colima. Jalisco: BM 1892.2.8.75, holotype, Lake Chapala; SU 6158, holotype of *C. crystallina*, Lake Chapala; SU 6203 (4), Lake Chapala at Ocotlán; SU 6160, holotype of *C. ocotlanae*, Lake Chapala; TU 40812 (3), Lake Chapala, about 0.2 mi. E of El Fuerte at E end of lake; TU 40872 (1), TU 40820 (1), Río Grande de Santiago at Poncitlán; TU 40838 (144), TU 31986 (13), TU 40829 (3), Lake Chapala at Ajijic; TU 31971 (24), TU 31970 (1), Lake Chapala 15.8 mi. W of town of Chapala at Jocotepec; TU 31980 (3), Lake Chapala 1.6 mi. W town of Chapala; UMMZ 179741 (51), Lake Chapala at Tuxcueca; FMNH 3660 (3), Ocotlán; USNM 130933 (5), USNM 130934 (4), Lake Chapala (?); USNM 126981 (2), Lake Chapala. Michoacán: FMNH 3671 (1), La Palma.

Specimens of unknown localities.—USNM 130924 (1); USNM 130925 (1); USNM 130937 (2).

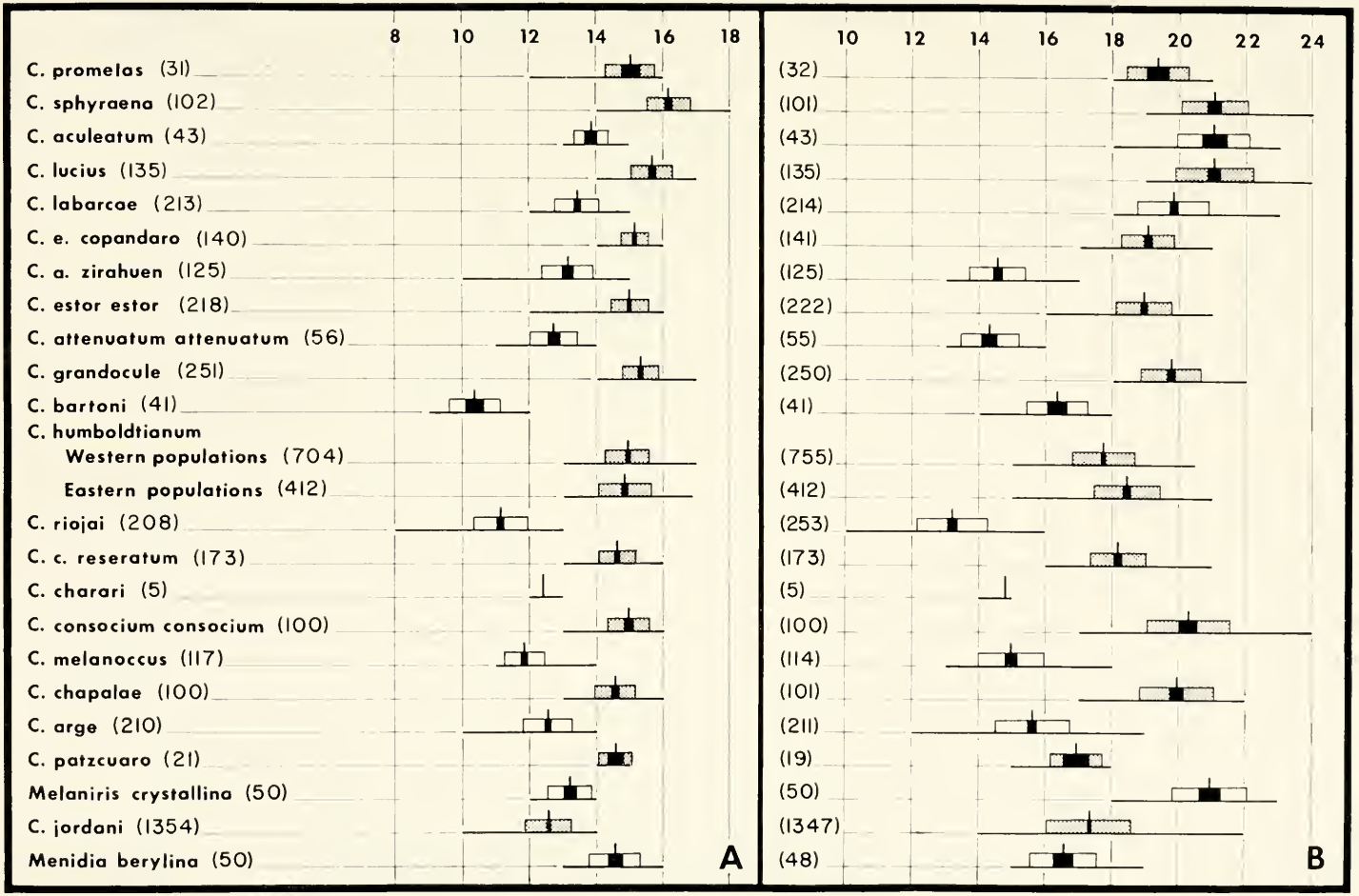
CHIROSTOMA SPHYRAENA BOULENGER
Fig. 17b

Chirostoma sphyraena Boulenger, 1900:54, holotype: BM 1892.2.8.77, type locality: Lake Chapala; Jordan and Snyder, 1899:137; Meek, 1902:116, 1904:177, Fig. 59; Regan, 1906–08:63, Tab. IX, Fig. 2; Jordan and Hubbs, 1919:80, Figs. 35, 36; Jordan, Evermann and Clark, 1928:251; Cuesta Terron, 1931:240; De Buen, 1940c:50, 1943:212, 1945:526, 1946a:279, 1946b:115; Schultz, 1948:31; Alvarez, 1950:102, 1970:126; Alvarez and Cortés, 1962:127; Minckley, 1965:73. *Chirostoma diazi* Jordan and Snyder, 1899:137; Jordan and Evermann, 1896–1900:3161; Regan, 1906–08:62; Jordan and Hubbs, 1919: 80, Fig. 32; Jordan, Evermann and Clark, 1928:251; De Buen, 1940c:50, 1943:212, 1945:527, 1946a:279, 1946b:115; Schultz, 1948:31; Alvarez, 1950a:102, 1970:125; Alvarez and Cortés, 1962:127. *Chirostoma lermae* Jordan and Snyder, 1899:142; Meek, 1902:116, 1904:179, Fig. 61.

Diagnosis.—Predorsal scales, 56–111; interdorsal scales, 8–29; gill rakers, 23–28; snout length, 10.2–12.9 in percent of standard length; mandible length, 12.3–15.2; pointed snout included by slightly projecting lower jar; teeth large, canine-like; body slender, barracuda-like.

→

Figure 8. Comparison of the number of (A) pectoral fin rays and (B) anal fin rays in *Menidia beryllina*, *Melaniris crystallina* and *Chirostoma*. See legend of Fig. 5 for explanation of the diagrams.


8 10 12 14 16 18
C. promelas (31)
C. sphyraena (102)
C. aculeatum (43)
C. lucius (135)
C. labarcae (213)
C. e. copandaro (140)
C. a. zirahuen (125)
C. estor estor (218)
C. attenuatum attenuatum (56)
C. grandocule (251)
C. bartoni (41)
C. humboldtianum
Western populations (704)
Eastern populations (412)
C. riojai (208)
C. c. reseratum (173)
C. charari (5)
C. consocium consocium (100)
C. melanoccus (117)
C. chapalae (100)
C. arge (210)
C. patzcuaro (21)
Melaniris crystallina (50)
C. jordani (1354)
Menidia berylina (50)
A
10 12 14 16 18 20 22 24
(32)
(101)
(43)
(135)
(214)
(141)
(125)
(222)
(55)
(250)
(41)
(755)
(412)
(253)
(173)
(5)
(100)
(114)
(101)
(211)
(19)
(50)
(1347)
(48)
B

Description.—Largest specimen examined 203 mm S.L.; head large, triangular; premaxillaries produced anteriorly; teeth in bands on premaxillaries with those placed anteriorly and medially enlarged, in two or three irregular rows on the dentaries with those in the outer row enlarged, none on the vomer or palatines; scale margins laciniate; predorsal scales crowded; lateral line scales with canals; pectoral fins moderately long and pointed.

Remarks.—There are indications that *C. sphyraena* hybridizes or introgresses with *C. lucius.* Most specimens of *C. lucius* have small teeth carried on a rather wide lower jaw. Some, however, have very large teeth on a jaw tending to be narrow and pointed as in *C. sphyraena.* These individuals were rare during the summer of 1963 but more common during the spring of 1969 when the level of Lake Chapala was much higher and the large silversides more abundant.

Range.—Lake Chapala, Jalisco–Michoacán and the Río Grande de Santiago at Poncitlán, Jalisco. I regard the locality "Colima," USNM 130918, as an error. The specimen probably came from Lake Chapala.

According to Minckley (1965), *C. sphyraena* and another unidentified *Chirostoma* have been introduced into the Río Conchos, Chihuahua.

Material examined.—Jalisco: BM 1892.2.-8.77, holotype, Lake Chapala; SU 6157, type of *C. diazi,* Lake Chapala (Market of Guadalajara); SU 6200 (3), market, Guadalajara; SU 6159, type of *C. lermae,* Lake Chapala (market of Guadalajara); SU 6212 (3), market, Guadalajara; TU 40837 (106), TU 31985 (24); Lake Chapala 4.9 mi. W town of Chapala at Ajijic; TU 40875 (3), Lake Chapala, 15.8 mi. W of Chapala at Jocotepec; UMMZ 179743 (4), Lake Chapala at Tuxcueca; UMMZ 167721 (12) NW side Lake Chapala at 5,000 ft.

CHIROSTOMA PROMELAS JORDAN AND SNYDER

Chirostoma promelas Jordan and Snyder, 1899: 136, Fig. 14, holotype: SU 6156, type locality, Lake Chapala (market of Guadalajara, Jalisco); Jordan and Evermann, 1896–1900: 3160; Pellegrin, 1901:205; Evermann and Goldsborough, 1901:152; Meek, 1902:115, 1904:177; Regan, 1906–08:62; Jordan and Hubbs, 1919:79, Figs. 29, 30; Jordan, Evermann and Clark, 1928:251; Cuesta Terron, 1931:240; De Buen, 1940c:50, 1943:212; Schultz, 1948:31. *Otalia promelas,* De Buen, 1945:529, 1946a:279, 1946b:115; Alvarez, 1950a:99, 1970:128; Alvarez and Cortés, 1962:128.

Diagnosis.—Lower jaw equal to or included by snout; snout pigmented black.

Description.—Largest specimen examined 165 mm S.L.; head triangular, jaw moderately long; snout long and pointed; premaxillaries produced anteriorly; teeth large, in bands, directed sharply posteriorly, none on vomer or palatines. Scale margins laciniate; predorsal scales crowded; lateral line scales with canals; pectoral fins moderately long and pointed.

Remarks.—*C. promelas* is most closely related to *C. sphyraena,* but has a shorter mandible (Fig. 12).

Range.—Lake Chapala, Jalisco–Michoacán, Río Grande de Santiago at Poncitlán, Jalisco.

Material examined.—Jalisco: SU 6156, holotype, market of Guadalajara (Lake Chapala); UMMZ 167723 (1), NW side of Lake Chapala at 5,000 ft. el.; UMMZ 173542 (3), Lake Chapala, N shore 0.5 mi. W town of Chapala at village of Manglar; UMMZ 179719 (1), flooded edge of Lake Chapala ca. 1 mi. S Ocotlán near source of Río Grande de Santiago; UMMZ 179740 (1), Lake Chapala at Tuxcueca on S side of lake; LB 4116 (4), UMMZ 124466 (1), Lake Chapala; FMNH 3656 (3), Ocotlán; TU 40843 (11), TU 31987 (1), Lake Chapala 4.8 mi. W town of Chapala at Ajijic; TU 40823 (1), Río Santiago at Poncitlán; TU 40848 (1), Lake Chapala at San Juan Tecomatlán; UMMZ 197649 (1), Lake Chapala 3.8 mi. W Ajijic. Michoacán: FMNH 3664 (9), La Palma.

The Arge Group

Description.—Lateral line scales usually with pores; scale margins usually smooth; median lateral scales, 36–51; predorsal scales, 15–32; interdorsal scales, 1–8; gill rakers, 12–26; vertebrae, 35–43; pectoral fin rays, 8–15; anal fin rays, 10–19 with two species reaching 23. The species range in size from small to moderately large and include: *C. arge, C. melanoccus, C. riojai, C. charari, C. attenuatum, C. bartoni, C. labarcae* and *C. aculeatum.*

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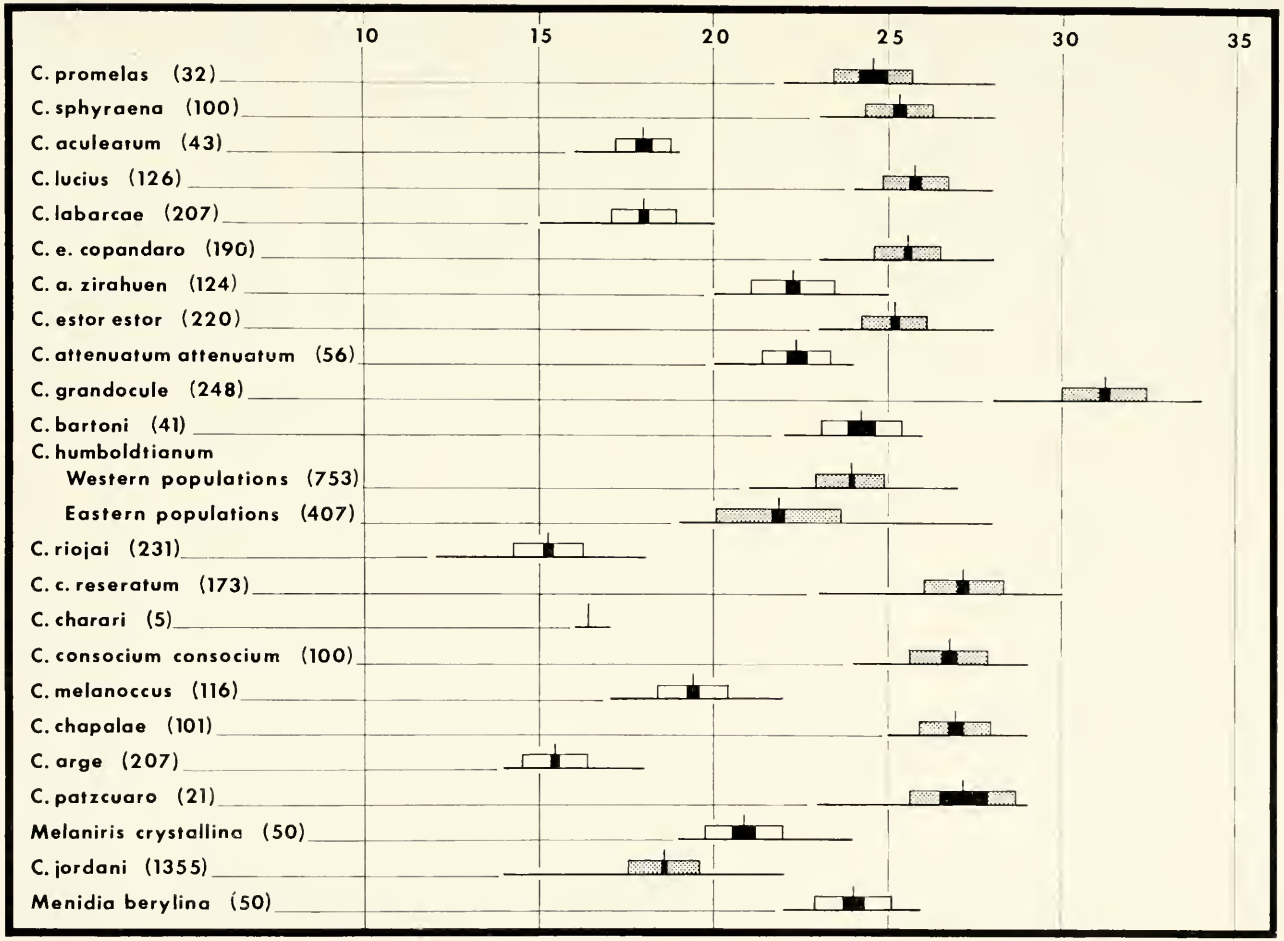
Figure 9. Comparison of the number of gill rakers in *Menidia berylina, Melaniris crystallina* and *Chirostoma.* See legend of Fig. 5 for explanation of the diagrams.


10
15
20
25
30
35
C. promelas (32)
C. sphyraena (100)
C. aculeatum (43)
C. lucius (126)
C. labarcae (207)
C. e. copandaro (190)
C. a. zirahuen (124)
C. estor estor (220)
C. attenuatum attenuatum (56)
C. grandocule (248)
C. bartoni (41)
C. humboldtianum
Western populations (753)
Eastern populations (407)
C. riojai (231)
C. c. reseratum (173)
C. charari (5)
C. consocium consocium (100)
C. melanoccus (116)
C. chapalae (101)
C. arge (207)
C. patzcuaro (21)
Melaniris crystallina (50)
C. jordani (1355)
Menidia berylina (50)

CHIROSTOMA ARGE (JORDAN AND SNYDER) Fig. 16c

Eslopsarum arge Jordan and Snyder, 1899:133, holotype: SU 6154, type locality: Río Verde near Aguascalientes, Aguascalientes; Jordan and Evermann, 1896–1900:3158; De Buen, 1945:504, 1946b:114. *Chirostoma arge*, Meek, 1902:112, 1904:171, 1907:156; Regan, 1906–08:59; Jordan and Hubbs, 1919:71, Fig. 23; Jordan, Evermann and Clark, 1930:250; Cuesta Terron, 1931:238; De Buen, 1940c: 48; Schultz, 1948:31; Alvarez, 1950a:101, 1970:125.

Diagnosis.—Gill rakers, 14–18; snout length, 6.4–8.5 in percent of standard length; length of caudal peduncle, 21.4–25.9; snout blunt, never angular in profile or pointed; teeth large, present on upper lip, easily visible or felt when mouth is closed; specimens from the Río de la Laja may have black on fins (Fig. 16c) and lateral line scales with canals as well as pores.

Description.—Maximum length around 65 mm S.L.; body relatively deep; head subtriangular; snout equal to or included by lower jaw; teeth in bands, outer members greatly enlarged, none on vomer or palatines; scale margins smooth; predorsal scales not crowded; lateral line usually in the form of pores (see *Diagnosis*); pectoral fins small, rounded or weakly pointed.

Remarks.—The Lake Chapala population of *C. arge* has the following frequency distribution of vertebrae: 38 (4 specimens), 39 (18), 40 (6), 41 (1). These numbers are generally higher than any of the other populations of the species and were not included in the data of Fig. 10. The populations in the Río de la Laja differ most trenchantly from those in the Río de Aguascalientes in the height of the anal fin (Fig. 14).

Range.—Headwaters of the Río Verde (Río de Aguascalientes) and the Río la Laja; Lake Chapala; tributaries to the lower Río Lerma (Fig. 1).

Material examined.—Aguascalientes: SU 6154, holotype, ANSP 26845–911 (17), Río Verde near Aguascalientes. Guanajuato: UMMZ 197622 (186), Río de la Laja 4 mi. S San Miguel de Allende in impoundment; UMMZ 197623 (169), Río de la Laja, below dam just S Empalme Escobedo; FMNH 5565 (50), San Miguel de Allende. Jalisco: FMNH 73319 (40), Lagos; UMMZ 179745 (12), Lake Chapala on S side of lake at Tuxcueca; UMMZ 173541 (28), Lake Chapala 0.5 mi. W town of Chapala at Village of Manglar; UMMZ 172201 (34), trib. to Río Verde at Cuarenta, 15 mi. NE Lagos de Moreno, el. 6,500 ft.; UMMZ 179762 (118), Río de Aguascalientes at E edge of Belén del Refugio; TU 40816 (9), E end of Lake Chapala ca. 4 mi. W town of Cuitzeo at end of road; TU 40830 (33), TU 40842 (4), Lake Chapala at Ajijic; TU 40834 (3), Lake Chapala; S shore of Isla de los Alacranes. Michoacán: UMMZ 197616 (1), trib. to Río Lerma on N side of Tanhuato.

CHIROSTOMA MELANOCCUS ALVAREZ

Chirostoma melanoccus Alvarez, 1963b:127, holotype: P 731, type locality: San Juanico dam, Michoacán, 1970:125.

Diagnosis.—Median lateral scales, 39–45; gill rakers, 17–22; anal fin rays, 13–18; eye length, 6.0–6.8 in percent of standard length; snout to origin of first dorsal fin, 48.1–51.3; snout blunt, never angular in profile; teeth minute; lateral line scales always with pores.

Description.—Maximum length about 65 mm S.L.; body slender; head subtriangular; teeth in two or three rows on the premaxillaries and dentaries, none on vomer or palatines; scale margins smooth; predorsal scales not crowded; pectoral fins moderately long, rounded.

Range.—Known only from the type locality, San Juanico dam near Cotija, Michoacán (Fig. 1).

Material examined.—Michoacán: TU 40867 (69), TU 31945 (46), San Juanico dam, 5 mi. SE Cotija.

CHIROSTOMA RIOJAI SOLORZANO AND LOPEZ

Chirostoma riojai Solórzano and López, 1965: 145, holotype: LB 1820, type locality: Lake Santiago Tilapa, Mexico State; Alvarez, 1970: 125. *Chirostoma bartoni*, Evermann and Goldsborough, 1901:152; Meek, 1902:112, 1904:172; Regan, 1906–08:58 (in part); Jordan and Hubbs, 1919:72 (in part); De Buen, 1940c:49 (in part); Romero, 1967:68.

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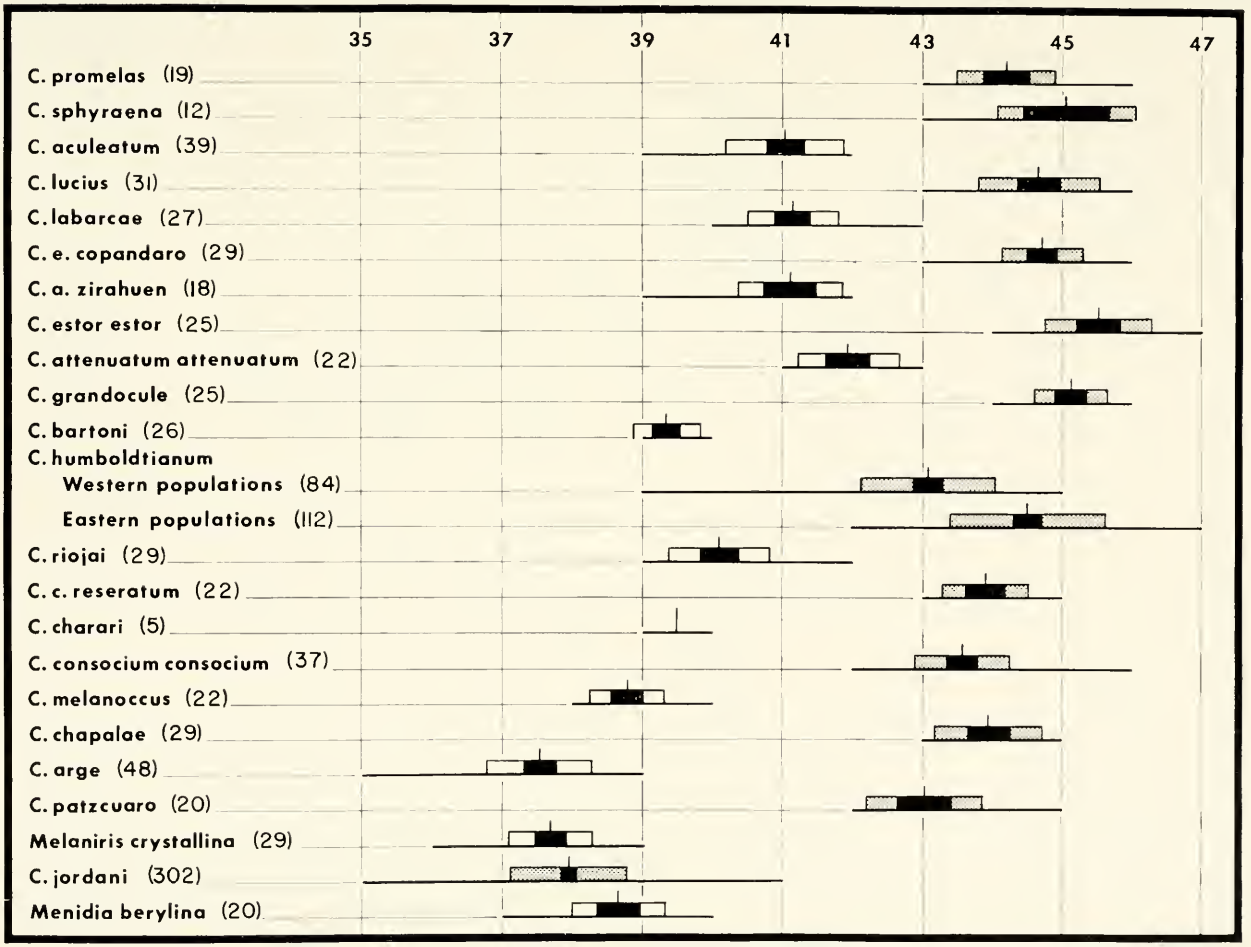
Figure 10. Comparison of the total number of vertebrae in *Menidia berylina*, *Melaniris crystallina* and *Chirostoma*. See legend of Fig. 5 for explanation of the diagrams.


35
37
39
41
43
45
47
C. promelas (19)
C. sphyraena (12)
C. aculeatum (39)
C. lucius (31)
C. labarcae (27)
C. e. copandaro (29)
C. a. zirahuen (18)
C. estor estor (25)
C. attenuatum attenuatum (22)
C. grandocule (25)
C. bartoni (26)
C. humboldtianum
Western populations (84)
Eastern populations (112)
C. riojai (29)
C. c. reseratum (22)
C. charari (5)
C. consocium consocium (37)
C. melanoccus (22)
C. chapalae (29)
C. arge (48)
C. patzcuaro (20)
Melaniris crystallina (29)
C. jordani (302)
Menidia berylina (20)

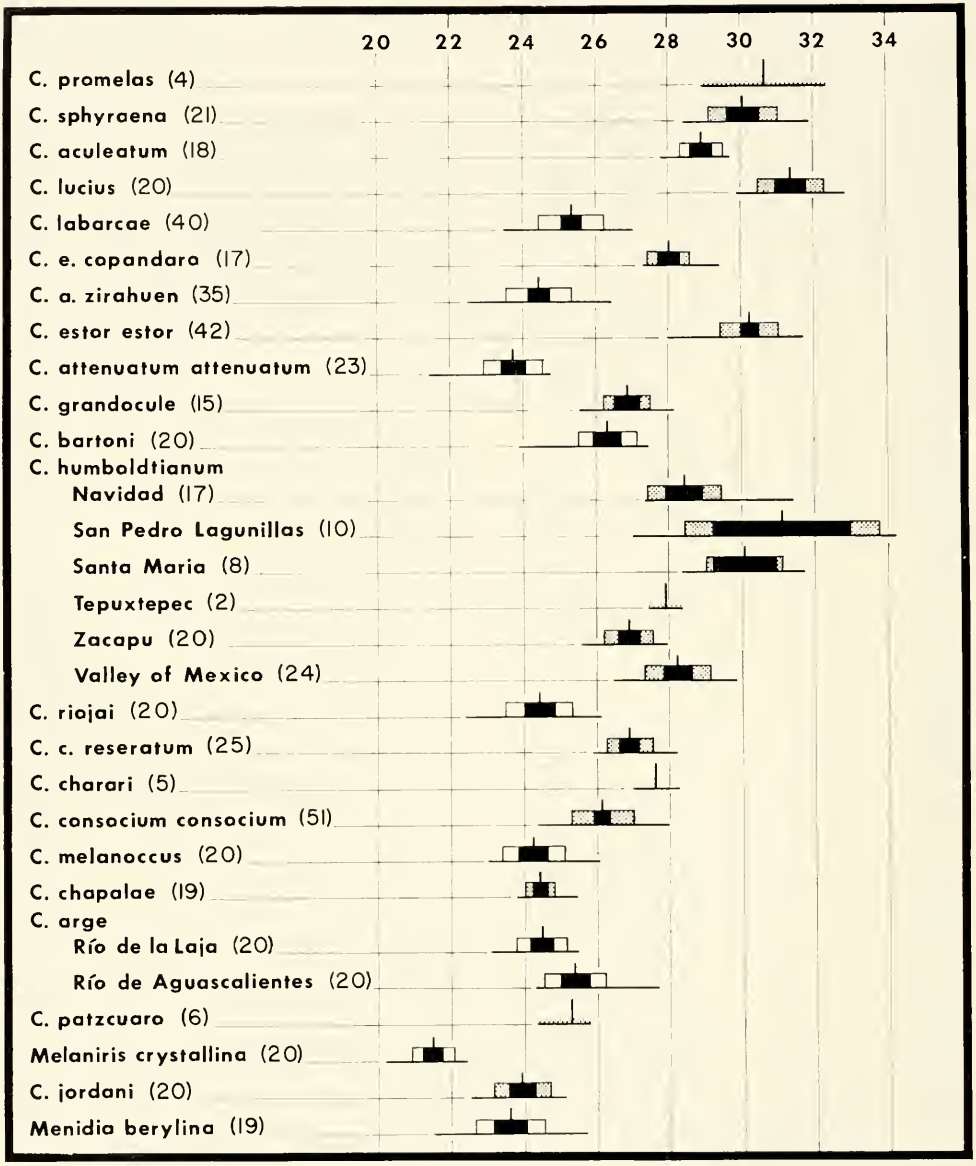


Figure 11. Comparison of head length, expressed as a percent of standard length, in *Menidia berylina*, *Melaniris crystallina* and *Chirostoma*. See legend of Fig. 5 for explanation of the diagrams.

Chirostoma bartoni bartoni, Alvarez, 1950: 100 (in part), 1970:124 (in part); Alvarez and Cortés, 1962:123 (in part). *Eslopsarum bartoni bartoni* De Buen, 1945:506 (in part), 1946b:114 (in part).

Diagnosis.—Gill rakers, 12–18; anal rays, 10–16; snout to origin of first dorsal fin, 45.2–48.4 in percent of standard length; eye length, 5.1–6.0; snout blunt, never angular in profile; premaxillaries not enlarged and produced anteriorly or laterally decurved as in *C. charari*; teeth small, none outside mouth as in *C. arge*; scale margins smooth, no tendency towards laciniation predorsally.

Description.—Maximum length about 74 mm S.L.; body relatively deep; snout equal to or included by lower jaw; teeth in bands,

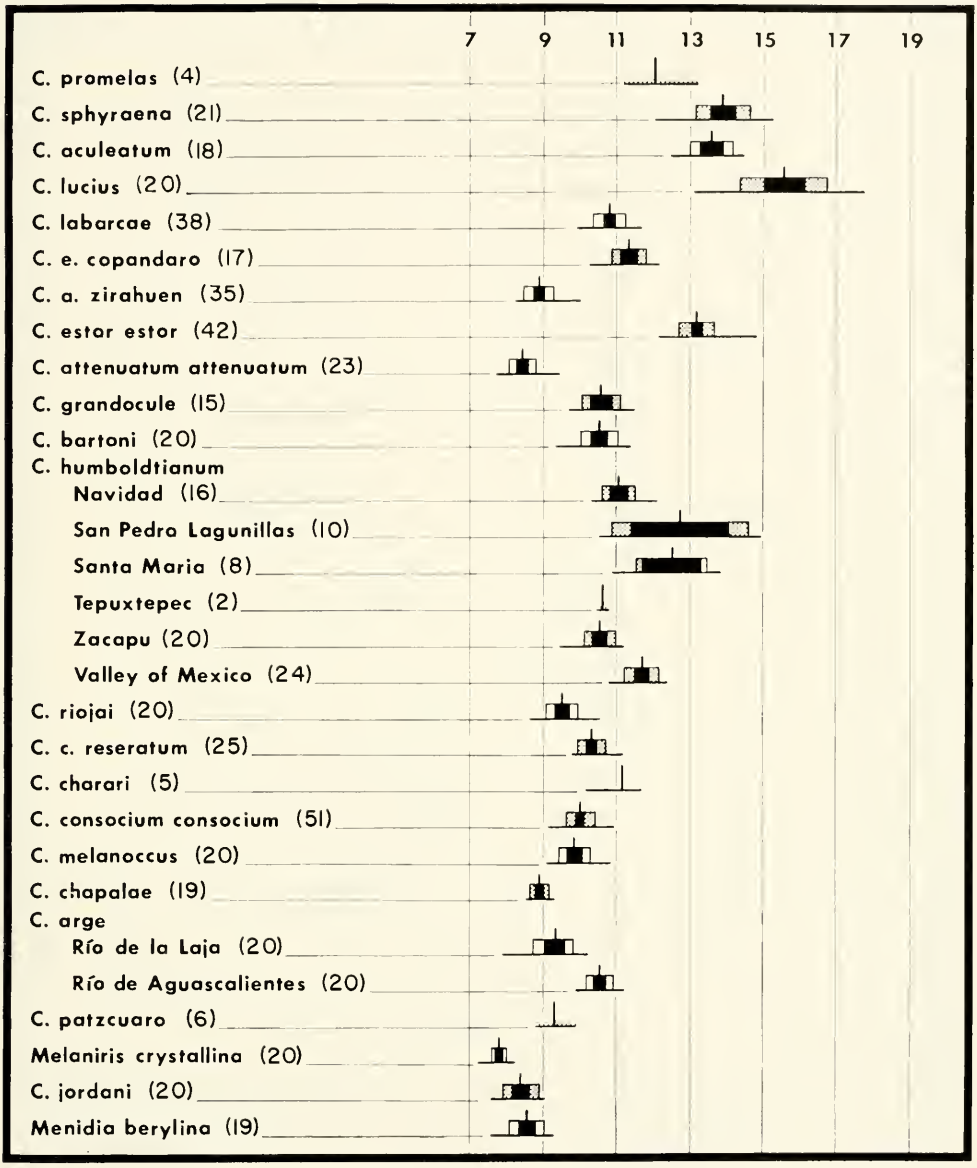


Figure 12. Comparison of mandibular length, expressed as a percent of standard length, in *Menidia berylina*, *Melaniris crystallina* and *Chirostoma*. See legend of Fig. 5 for explanation of the diagrams.

outer members not enlarged, none on vomer or palatines; lateral line scales with pores; predorsal scales not crowded; pectoral fins small, rounded.

Range.—Headwaters of the Río Lerma and Lakes in the Valley of Toluca, Mexico State (Fig. 1).

Material examined.—Mexico: TU 40173 (2), paratypes, Laguna de Santiago Tilapa; UMMZ 172175 (75) Laguna Agua Blanca, 14 mi. by road SW Toluca; TU 31867 (71), Río Lerma, 1.5 mi. W town of Lerma, hwy. 15; UMMZ 197634 (1), TU 31871 (86), Río Lerma, 12.5 mi. NW Toluca, hwy. 55; USNM 126980 (10), USNM 50228 (32), Lake Lerma; UMMZ 197632 (566), Río Lerma just below Alzate Dam, 15.2

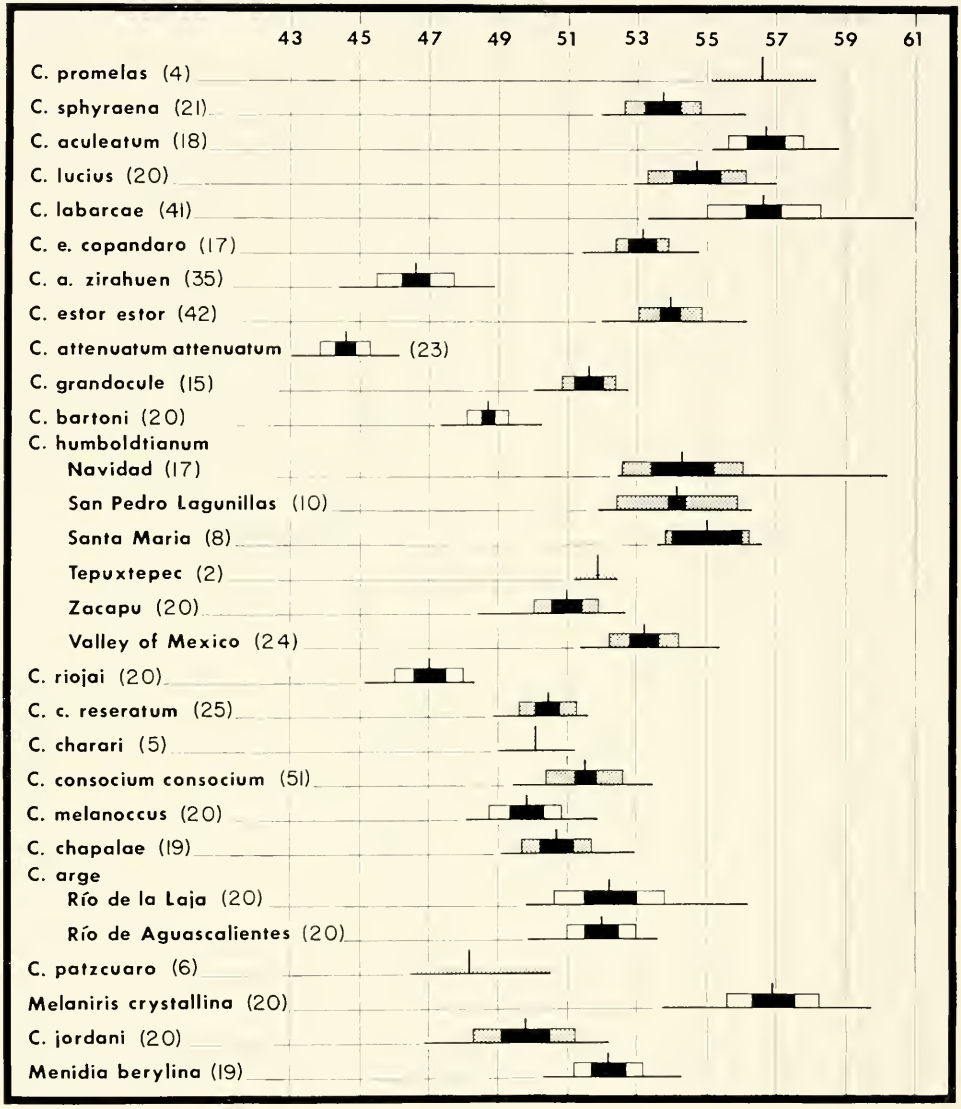


Figure 13. Comparison of the distance from the snout to the origin of the first dorsal fin, expressed as a percent of standard length, in *Menidia berylina*, *Melaniris crystallina* and *Chirostoma*. See legend of Fig. 5 for explanation of the diagrams.

mi. N Toluca, hwy. 55; UMMZ 197633 (78); behind Ignacio Ramirez Dam, W hwy. 55, 20.4 mi. N Toluca.

CHIROSTOMA CHARARI (DE BUEN)

Eslopsarum bartoni charari De Buen, 1945: 509, holotype: lost, originally deposited in the collection of the Pátzcuaro Limnological Station, type locality: Río Grande de Morelia at Morelia, Michoacán, 1946b:114. *Chirostoma bartoni charari*, Schultz, 1948:31; Alvarez, 1950a:100, 1970:124; Alvarez and Cortés, 1962:123. *Chirostoma bartoni*, De Buen, 1943:212, 1944a:264. *Chirostoma bartoni* var. (?) De Buen, 1941a:24.

Diagnosis.—Gill rakers, 16–17; anal rays, 14–15; eye length, 6.6–7.2 in percent of standard length; snout length, 8.6–9.7; snout subtriangular; premaxillaries enlarged, produced anteriorly and decurved laterally.

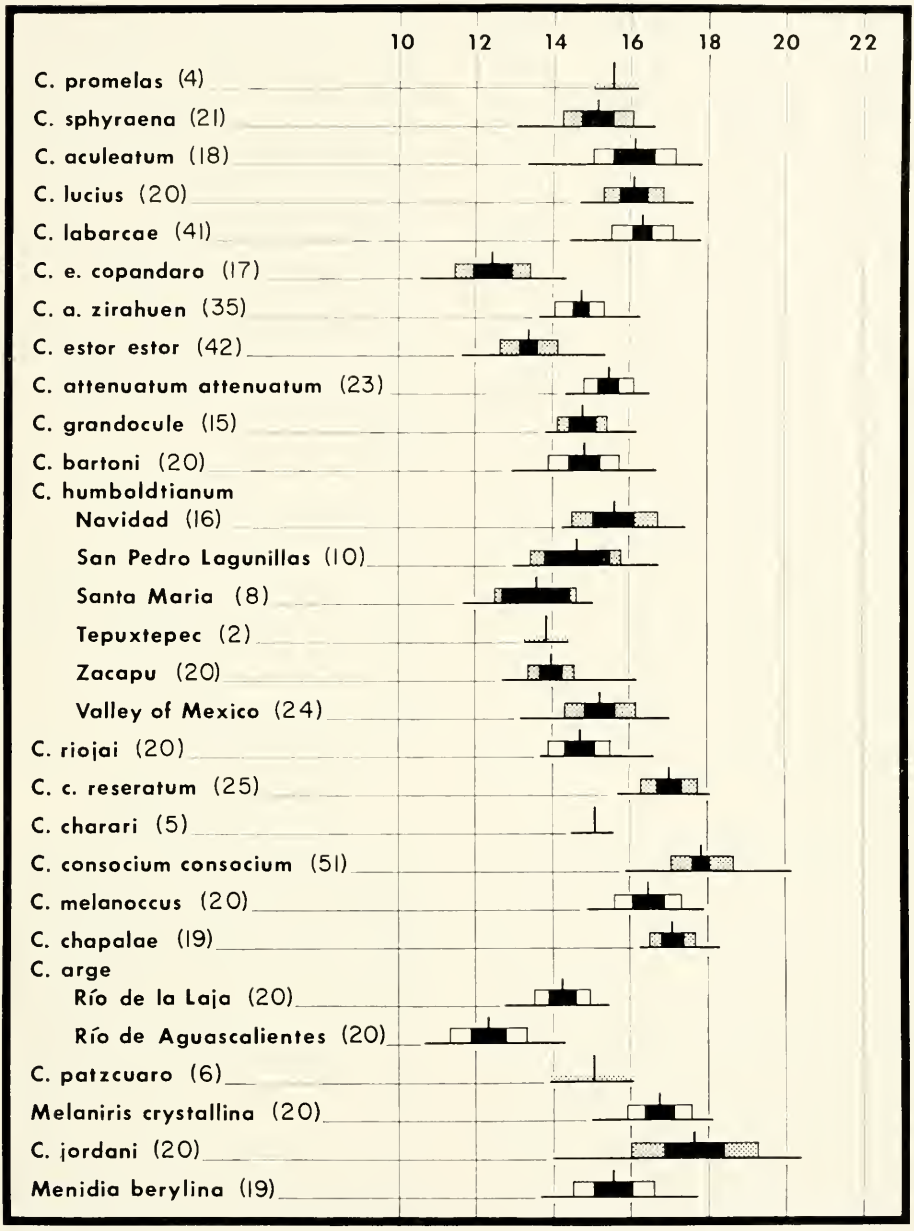


Figure 14. Comparison of anal fin height, expressed as a percent of standard length, in *Menidia berylina*, *Melaniris crystallina* and *Chirostoma*. See legend of Fig. 5 for explanation of the diagrams.

Description.—Largest specimen examined 64.8 mm S.L.; body slender: snout long, weakly pointed; teeth moderately large, relatively few in number, in one or two irregular rows on dentaries and premaxillaries with the outer members slightly enlarged, none on vomer or palatines; scale margins smooth; lateral line scales with pores; predorsal scales not crowded; pectoral fins small, rounded. Proportional measurements of five specimens of *C. charari* (TU 31911, 57.9–64.8 mm S.L.) expressed in thousandths of the

standard length are given below. The range is followed by the mean. Distance from snout to origin of first dorsal fin: 490–513, 501; distance from snout to origin of second dorsal fin: 634–662, 646; distance from snout to origin of pelvic fins: 394–410, 400; distance from snout to origin of anal fin: 555–572, 567; head length: 270–283, 276; postorbital head length: 117–130, 122; eye length: 66–72, 69; snout length: 86–97, 90; mandible length: 102–117, 112; least depth of caudal peduncle: 76–84, 81; length of caudal peduncle: 234–250, 241; height of second dorsal fin: 145–164, 153; length of base of anal fin: 187–207, 196; height of anal fin: 145–158, 151; length of pectoral fin: 151–169, 160.

Remarks.—Although the type is lost, I recognize this species on the basis of five specimens, mentioned above, which seem to agree fairly well with De Buen's descriptions (1941a, 1945). They were collected in a spring-fed lake in the same drainage about five miles from the type locality.

Range.—Río Grande de Morelia basin in the vicinity of Morelia, Michoacán (Fig. 1).

Material examined.—Michoacán: TU 31911 (5), spring-fed lake just N Balneario Cointzio ca. five air miles W Morelia.

CHIROSTOMA ATTENUATUM ATTENUATUM MEEK

Chirostoma attenuatum Meek, 1902:112, holotype: FMNH 3631, type locality: Lake Pátzcuaro, Michoacán, 1904:173, Fig. 55; Cuesta Terron, 1931:241. *Chirostoma samani* Cuesta Terron, 1931:241. *Chirostoma bartoni*, Regan, 1906–08:58, Tab. 10, Fig. 2 (in part); Jordan and Hubbs, 1919:72, Fig. 24 (in part); Jordan, Evermann and Clark, 1928: 250 (in part); De Buen, 1940b:18, Fig. 4 (in part), 1941d:73 (in part), 1943:212 (in part); Martin del Campo, 1940:483 (in part). *Chirostoma bartoni bartoni*, De Buen, 1941a: 24 (in part), 1941c:7 (in part), 1942:41 (in part), 1944a:269 (in part); Schultz, 1948:31 (in part); Alvarez, 1950a:100 (in part), 1970: 124 (in part); Alvarez and Cortés, 1962:123 (in part). *Chirostoma bartoni* var. *attenuatum*, De Buen, 1940b:22, 1949c:49. *Chirostoma bartoni* var. *janitzio*, De Buen, 1940a: 306, 1940b:22, 1940d:7, Figs. 1–14, 1941d: 76; Martin del Campo, 1940:483. *Eslopsarum bartoni bartoni*, De Buen, 1945:506 (in part), 1946b:114 (in part).

Diagnosis.—Median lateral scales, 43–51; gill rakers, 20–24; distance from snout to origin of first dorsal fin, 43.1–46.2 in percent of standard length; length of caudal peduncle, 26.6–30.2.

Description.—Maximum length about 89 mm S.L.; body slender; snout blunt; teeth small, in bands, none on vomer or palatines; scales with smooth edges; predorsal scales not crowded; lateral line scales with pores; pectoral fins short, rounded.

Remarks.—See Remarks under *C. bartoni*. The biology of this species has been discussed by Solórzano (1961).

C. samani Cuesta Terron is synonymized with *C. attenuatum attenuatum* because of its smooth scale margins even though it has a high number of gill rakers (26). The species is known only from the original description.

Range.—Known only from the type locality, Lake Pátzcuaro, Michoacán.

Material examined.—Michoacán: FMNH 3631, holotype; USNM 55782 (2), FMNH 3632 (12), paratypes, all from Lake Pátzcuaro; TU 40851 (32), Lake Pátzcuaro, W of Ihuatzio; TU 40881 (14), Lake Pátzcuaro between Napizaro, Jacuaro and Erongaricuaro; TU 40858 (10), Lake Pátzcuaro, S shore of Isla de Yuñen; USNM 187617 (2), Pátzcuaro; USNM 203145 (7), Lake Pátzcuaro.

CHIROSTOMA ATTENUATUM ZIRAHUEN MEEK

Chirostoma zirahuen Meek, 1902:114, holotype: FMNH 3609, type locality: Lake Zirahuén, Michoacán, 1904:174, Fig. 57; Jordan and Hubbs, 1919:72, Fig. 25; Jordan, Evermann and Clark, 1928:250; Cuesta Terron, 1931: 239; De Buen, 1940c:49. *Chirostoma bartoni*, Regan, 1906–08:58, Tab. X, Fig. 2 (in part). *Chirostoma bartoni zirahuen*, De Buen, 1941a: 23, 1941c:7, 1943:214, 1944b:21; Schultz, 1948:31; Alvarez, 1950a:100, 1970:124; Alvarez and Cortés, 1962:123. *Eslopsarum bartoni zirahuen*, De Buen, 1945:508, 1946b: 114.

Diagnosis.—*C. attentuatum zirahuen* is best distinguished from the nominate form (ranges and means in parentheses) by a greater number of median lateral scales, 48–70, $\bar{x} = 58.1$ (43–51, $\bar{x} = 46.4$); greater number of predorsal scales, 19–32, $\bar{x} = 25.2$ (16–24, $\bar{x} = 19.3$); greater snout to first dorsal fin origin distance, 44.4–48.9, $\bar{x} = 46.6$ (43.1–46.2, $\bar{x} = 44.6$) in percent of standard length. Differs from *C. bartoni* by having a greater number of median lateral scales (42–49, $\bar{x} = 44.8$); greater number of pectoral fin rays, 10–15, $\bar{x} = 13.1$ (9–12,

$\bar{x} = 10.4$); fewer anal fin rays, 13–17, $\bar{x} = 14.5$ (14–18, $\bar{x} = 16.3$). Differs from all other *Chirostoma* by the number of median lateral scales, predorsal scales and anal fin rays; snout to pelvic fin origin distance, 37.3–40.8; least depth caudal peduncle, 6.5–8.1; length caudal peduncle, 24.0–30.1.

Description.—Largest specimen examined 88 mm S.L.; body slender; head subtriangular; snout blunt; premaxillaries not produced anteriorly as in *C. charari*, smoothly decurved laterally, becoming angular in large specimens; teeth small, in two irregular rows or narrow bands, none on vomer or palatines; scale margins smooth; predorsal scales not crowded; lateral line scales with pores, much reduced in some specimens; pectoral fins short, rounded.

Remarks.—Ripe males and females were collected on March 30, 1964. Both sexes were a bronze color. See also Remarks under *C. bartoni.*

Range.—Known only from the type locality, Lake Zirahuén, Michoacán.

Materal examined.—Michoacán: FMNH 3609, holotype; ANSP 90854 (2), paratypes; TU 31918 (266); UMMZ 187669 (8). All from Lake Zirahuén, 19 mi. S Pátzcuaro.

CHIROSTOMA BARTONI JORDAN AND EVERMANN

Chirostoma bartoni Jordan and Evermann, 1896–1900:793, holotype: USNM 23136, type locality: "La Alberca," volcanic caldera W Valle de Santiago, Guanajuato; Regan, 1906–08:58, Tab. X, Fig. 2 (in part); Jordan and Hubbs, 1919:72, Fig. 24 (in part); Jordan, Evermann and Clark, 1928:250 (in part); De Buen, 1940b:18, Fig. 4 (in part), 1940c:49 (in part), 1943:212 (in part); Solórzano, 1961:15 (in part). *Chirostoma bartoni bartoni*, Alvarez, 1950a:100 (in part); Alvarez and Cortés, 1962:123 (in part). *Chirostoma humboldtianum*, Jordan, 1879: 299. *Chirostoma regani*, Martin del Campo, 1940:484 (in part). *Eslopsarum bartoni* Jordan and Evermann, 1895:330, 1896–1900: 2840. *Eslopsarum bartoni bartoni*, De Buen, 1945:506 (in part), 1946b:114 (in part).

Diagnosis.—Median lateral scales, 42–49; pectoral fin rays, 9–12; gill rakers, 22–26; mandible length, 9.4–11.5 in percent of standard length; length of caudal peduncle, 22.3–24.9; snout angular; jaw oblique.

Description.—Largest specimen examined 71 mm S.L.; body moderately slender; head triangular; snout pointed; premaxillaries moderately produced anteriorly; teeth in bands, occasionally present on vomer; scale margins smooth; predorsal scales not crowded; lateral line scales with pores; pectoral fins moderately long, rounded or slightly pointed.

Remarks.—*C. bartoni* is most closely related to *C. attenuatum attenuatum* and *C. a. zirahuen.* The species may be separated from the latter by its fewer number of median lateral scales (overlap of 2) and from the former by its higher number of predorsal scales (overlap of 4). When the following characters are compared, *C. a. attenuatum* and *C. a. zirahuen* always show a greater concordance: number of pectoral and anal fin rays, number of gill rakers on the first arch, snout, mandible, head, eye, postorbital head and caudal peduncle length, distance from snout to anal fin origin and least depth of caudal peduncle. *C. bartoni* also occasionally has teeth on the vomer. For these reasons, *C. bartoni* is retained as a species and *C. a. attenuatum* and *C. a. zirahuen* as subspecies.

Range.—Known only from the type locality, "La Alberca," an extinct volcanic caldera immediately W Valle de Santiago, Guanajuato (Fig. 1).

Material examined.—Guanajuato: USNM 23136, holotype; UMMZ 197624 (30), UMMZ 197638 (15). All from "La Alberca," caldera lake immediately W Valle de Santiago.

CHIROSTOMA LABARCAE MEEK

Fig. 18b

Chirostoma labarcae Meek, 1902:112, holotype: FMNH 3640, type locality: Río Lerma at La Barca, Jalisco, 1904:173; Jordan and Hubbs, 1919:71, Fig. 22; Jordan, Evermann and Clark, 1928:250; Cuesta Terron, 1931: 238; De Buen, 1940c:48, 1943:212; Schultz, 1948:31; Alvarez, 1950a:101, 1970:125; Alvarez and Cortés, 1962:122. *Chirostoma breve*, Regan, 1906–08:59 (in part). *Eslopsarum labarcae*, De Buen, 1945:503, 1946a: 277, 1946b:114.

Diagnosis.—Median lateral scales, 39–47; gill rakers, 15–20; length of caudal peduncle, 16.5–21.1 in percent of standard length; length of pectoral fin, 19.4–22.8; length of anal fin base, 21.7–28.3; head length, 23.5–27.0; snout length, 8.3–9.9; snout pointed; teeth small to large; scale margins weakly laciniate in predorsal region; lateral line scales with fine canals.

Description.—Largest specimen examined 85 mm S.L.; head triangular; premaxillaries produced anteriorly; teeth in irregular rows or band, outer members on dentaries large and canine-like as are those on medial portions of premaxillaries; predorsal scales not crowded; pectoral fins long and pointed.

Range.—Lake Chapala, Jalisco–Michoacán, Río Grande de Santiago at Poncitlán, Río Lerma at La Barca, Jalisco (Fig. 4).

Material examined.—JALISCO: FMNH 3640, holotype, Río Lerma at La Barca; UMMZ 179721 (1), Lake Chapala at Jamay, near E end of lake; UMMZ 179715 (13), flooded edge of Lake Chapala ca. 1 mi. S Ocotlán near source of Río Grande de Santiago; UMMZ 179747 (60), Lake Chapala at Tuxcueca on S side of lake; UMMZ 179709 (1), Lake Chapala at SW end opposite Ajijic; UMMZ 108641 (5), Río Grande de Santiago between Ocotlán and Lake Chapala, or outlet end of lake nearby; UMMZ 124467 (5), Lake Chapala; UMMZ 173539 (2), Lake Chapala, N shore 0.5 mi. W town of Chapala at village of Manglar; UMMZ 167722 (4), NW side, Lake Chapala, 5,000 ft. el.; TU 40831 (33), TU 40839 (35), TU 31988 (6), Lake Chapala 4.8 mi. W of town of Chapala at Ajijic; TU 31966 (22), Lake Chapala 1.6 mi. W town of Chapala; TU 40821 (14), TU 31958 (4), Río Santiago at Poncitlán; TU 40814 (21), Lake Chapala 0.2 mi. E of El Fuerte at E end of lake; TU 40817 (2), Lake Chapala 1–2 mi. W of town of Cuitzeo at end of road, NE end of lake; TU 40835 (44), Lake Chapala, Isla de los Alacranes, S shore in area especially cleared by fisherman for throw net.

CHIROSTOMA ACULEATUM NEW SPECIES

Fig. 18a

Chirostoma jordani Woolman, 1894:62 (in part, misidentification). *Chirostoma arge*, Jordan and Hubbs, 1919:71 (in part, based on USNM 203107).

Holotype.—TU 40889, 85.00 mm standard length, collected along the south shore of Lake Yuriria 1.5 miles east of the town of Yuriria, Guanajuato, 1 August 1963 by commercial fishermen. Paratypes.—GUANAJUATO: TU 40864 (11), same data as holotype; USNM 205784 (3), USNM 205783 (5), Río Turbio 8 miles east of Pénjamo at highway 110 crossing. MICHOACÁN: UMMZ 197682 (2), USNM 205785 (19), tributary to the Río Lerma at the northeast end of the town of Tanhuato on the road to Yurécuaro, below small earthen dam. Two specimens bearing the same data as USNM 205785 have been deposited in the Instituto Nacional de Investigaciones Biológico Pesqueras, Laboratorio Biológico, México, D. F.

Other specimen.—GUANAJUATO: USNM 203107, Salamanca, removed from syntypes of *C. jordani* Woolman.

Diagnosis.—A *Chirostoma*, mostly closely related to *C. labarcae*, distinguished from all other members of the genus by having anal fin rays, 18–23; gill rakers, 15–21; mandible length, 12.5–14.5 in percent of standard length. Distinguished from *C. labarcae* (ranges, means and comments in parentheses) by having a longer head, 27.9–29.8, $\bar{x}$ = 28.9 (23.5–27.1, $\bar{x}$ = 25.4); longer snout, 10.1–12.1, $\bar{x}$ = 11.1 (8.3–9.9, $\bar{x}$ = 9.0); longer mandible, $\bar{x}$ = 13.6 (9.9–11.7, $\bar{x}$ = 10.8); premaxillary strongly decurved (weakly decurved).

Description.—A moderately large species, largest specimen examined 109.4 mm S.L., but according to fishermen reaching a length of 130–140 mm S.L.; body slender; snout long, pointed, included by lower jaw; teeth in two irregular rows on the dentaries, those along the outer edges large, canine-like, those immediately interior small, fine; teeth on the premaxillaries large but, with the exception of one or two canine-like on either side of the median symphysis, somewhat smaller than the large teeth on the dentaries; teeth absent from vomer and palatines; scale margins smooth or very weakly laciniate; predorsal scales not crowded; lateral line scales with canals. Proportional measurements are given in Table 1.

Remarks.—*C. aculeatum* inhabits lakes, rivers and small streams. All of my specimens were found in turbid water not less than two feet deep.

Range.—Lower reaches of the Río Lerma and tributaries (Fig. 4). According to Aurelio Solórzano (pers. comm.), *C. aculeatum* occurs in Lake Chapala at the mouth of the Río Lerma.

Etymology.—The name *aculeatum* is derived from the Latin meaning "sharp, pointed" and alludes to the species' snout.

Specimens of uncertain status.—TU 40844 (1) and TU 40876 (1), Lake Chapala, with the following counts, respectively: median lateral scales, 49, 48; predorsal scales, 32, 32; interdorsal scales, 5, 6; anal fin rays, 22, 19; gill rakers, 23, 22; total number of vertebrae, 43, 43. These specimens appear to be inter-

TABLE 1. Measurements of *Chirostoma aculeatum* expressed in thousands of the standard length; 52.0–109.4 mm S.L.; TU 40889 (1), TU 40864 (10), USNM 205783 (2), USNM 205784 (3), USNM 205785 (2).

		17 paratypes plus holotype			
	Holotype	Mean	Range	95% Conf. lim.	St'd dev.
Snout to first dorsal fin origin	567	567	552–588	5.4	10.8
Snout to second dorsal fin origin	703	700	686–783	4.0	8.0
Snout to pelvic fin origin	442	442	420–456	4.2	8.4
Snout to anal fin origin	593	586	567–607	5.5	10.1
Head length	288	289	279–298	2.9	5.8
Postorbital head length	116	128	116–136	2.3	4.7
Eye length	54	56	42–67	1.4	6.9
Snout length	115	111	101–121	2.6	5.3
Mandible length	145	136	125–145	2.9	5.9
Least depth of caudal peduncle	90	89	79–95	1.9	3.9
Length of caudal peduncle	173	180	160–193	5.1	10.2
Height of second dorsal fin	149	148	132–166	4.6	9.2
Length of anal fin base	241	249	236–269	5.0	10.0
Height of anal fin	158	161	134–179	5.4	10.9
Pectoral fin length	188	189	172–207	4.4	8.8

mediate between *C. labarcae* and/or *C. aculeatum* and one of the larger species in the lake.

PHYLOGENY OF *Chirostoma*

Before it is possible to discuss the evolution of the species of *Chirostoma*, the following topics must be considered: the primitive and derived characters for the genus, the primitive species within the genus and the possible ancestors.

Primitive and Derived Characters

Scale margins.—All juvenile specimens examined (less than 25 mm S.L.) had scales with smooth margins, including those species which as adults are characterized by laciniate scales. Laciniate scales are also associated with the most pronounced morphological specializations (see *C. lucius* and *C. promelas*). For these reasons, smooth-edged scales are considered primitive and laciniate derived.

Lateral line morphology.—All juvenile specimens examined had only pores in their lateral line scales, including those which as adults are characterized by lateral line scales with canals. There is also a correlation between morphological specialization and the presence of canals which cuts across the species groups (*C. lucius*, *C. sphyraena*, *C. promelas*, *C. labarcae* and *C. aculeatum*). Thus pores are considered primitive and canals derived.

Dentition.—Enlarged or canine-like teeth or the presence of teeth on the vomer, palatine, or lips are considered to represent a trophic specialization and thus are derived. One or two rows or a single band of small teeth on the dentaries and premaxillaries is considered the primitive state. It should be noted that there are indications that reversals of this character occur in *Chirostoma* (see arge group); it is not always possible to tell whether a species has a primitive dentition pattern or has undergone a character reversal and may be thus regarded as pseudoprimitive.

Pigmentation.—Distinct pigmentaion patterns other than a general darkening of the body resulting from local environmental conditions are so rare in *Chirostoma* that they are considered derived.

Meristic and morphometric characters.—In interpreting these characters, the assumption is made that *Chirostoma* evolved from a small marine atherinid, perhaps similar to *Menidia berylina* or *Melaniris crystallina*,

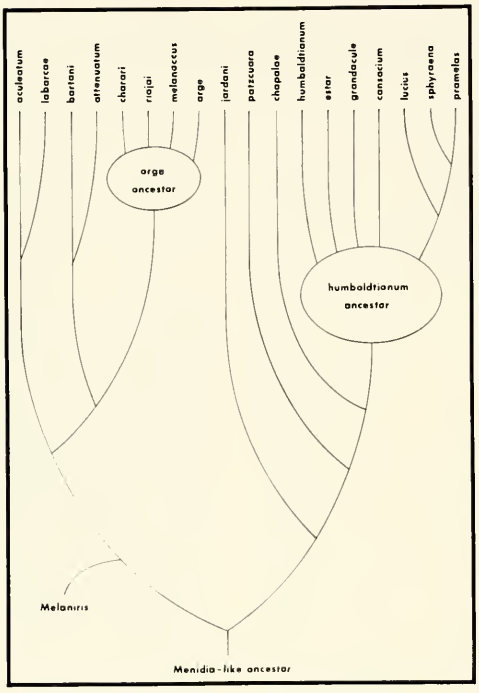


Figure 15. Phylogeny of *Chirostoma.*

which entered the streams and lakes of central Mexico during the Tertiary Period. As it is unlikely that a small ancestor would have very high meristic and morphometric values, species with low values are regarded as primitive for these characters. Care should be taken in interpreting individual cases, however, as extremely low values probably represent character reversals or specializations (e.g., the number of pectoral fin rays in *C. bartoni*, Fig. 8A, the number of anal fin rays in *C. riojai*, *C. aculeatum* and *C. labarcae*, Fig. 8B, the number of gill rakers in *C. riojai* and *C. grandocule*, Fig. 9, and the distance from the snout to the origin of the first dorsal fin in *C. riojai* and *C. attenuatum*, Fig. 13).

Modifications in the head region resulting from trophic specialization are considered derived as are increases in body size.

Primitive Species Within the Species Groups

The most primitive species within the jordani group is *C. jordani.* Its scale margins are usually smooth and canals in the lateral line scales are the exception rather than the rule. The species has no obvious trophic specializations other than a tendency towards an angular rather than a blunt snout. Where interspecific variation exists, *C. jordani* has low values for all morphometric and meristic characters. The species is also small.

Within the arge group, *C. bartoni*, *C. attenuatum*, *C. labarcae*, *C. aculeatum* and *C. charari* may be ruled out as primitive because of one or more high meristic values or obvious trophic specializations. The remaining three species have the following derived characters: *C. arge* has large teeth, some of which are present on the lip of the upper jaw. Specimens from the Río de la Laja have lateral line scales with pores and canals and black on the first and second dorsal, caudal and anal fins. *C. melanoccus* has 17–22 gill rakers on the first arch, an intermediate value for the arge group, and a range in eye length from 6.0 to 6.8 in percent of standard length which is surpassed only by *C. charari.* The species' minute teeth probably represent a character reversal. *C. riojai* has no obviously derived character states except for a low number of anal fin

rays and gill rakers which probably represent character reversals.

Morphological trends, whatever their significance in the jordani group, are not as apparent among the arge species. It is difficult to form a satisfactory hypothesis predicting which is the most primitive of the three species discussed above or to comment on possible relationships between both species groups without first examining the characteristics of related marine genera. This topic is considered next.

Possible Ancestors and the Origin of Chirostoma

A careful revision of the Atherinidae including an osteological analysis has never been made (Rosen, 1964). Any conclusions drawn regarding specific or generic relationships must be regarded as tentative at this time.

Atherinids are predominantly marine and brackish water coastal fishes. A number of species have entered fresh waters but with the exception of *Chirostoma* and perhaps *Basilichthys* and *Odontesthes* have undergone only a limited amount of diversification. This discussion will be limited to those genera occurring in Mexico and Central America.

Archomenidia and *Xenatherina* are probably restricted to the fresh waters of the Papaloapan, Coatzacoalcos and the Grijalva-Usumacinta basins. According to Schultz (1948) both genera have enlarged teeth projecting forward from the premaxillaries. The presence of this character and the species geographic position suggests that they are derived from *Melaniris*. I consider it unlikely that they are related to *Chirostoma* in spite of the fact that they are similar to *C. arge* in dentition.

Membras is too specialized to be a "persistent ancestor" of *Chirostoma* because of its laciniate scales, scale sheaths along the base of the second dorsal and anal fins and sensory grooves on the snout (Robbins, 1969, 1970).

Among the species of *Menidia* (including the nominal *Menidiella* Schultz), *M. berylina* ranges along the Atlantic and Gulf coasts from Massachusetts Bay to northern Vera Cruz. The species occurs in marine, brackish and freshwater habitats frequently in association with vegetation or floating debris. Specimens from Grand Isle, Louisiana are characterized by small teeth placed within the gape, a fairly high number of gill rakers (22–26), smooth scale margins and lateral line scales with canals becoming pores north of Virginia. Proportional measurements and counts tend to fall near the center of the range of variation for the arge group and the less specialized members of the jordani group (Figs. 5–14). A *Menidia berylina*-like stock could have easily given rise to *Chirostoma*.

The genus *Melaniris* is widely distributed along the Atlantic and Pacific coasts and in the fresh waters of Central America. On the east coast of Mexico it extends north to the Río Coatzacoalcos (Miller, 1966). Along the west coast *M. crystallina* (Fig. 16D) ranges from the Río Fuerte, Sonora south to the Río Grande de Santiago, Nayarit. In this drainage it extends inland to a point just above the mouth of the Río Verde (Briggs and Miller, 1960). Compared to the more primitive species of *Chirostoma* discussed above, specimens collected from the Río Grande de Santiago at the highway 15 crossing may be characterized by smooth-edged scales, lateral line scales with pores and canals, a high number of anal fin rays (Fig. 8B) and predorsal scales (Fig. 6) a relatively high number of gill rakers (Fig. 9) and the presence of rostral grooves (absent from all species of *Chirostoma*). Morphometrically, *M. crystallina* differs most in the distance from the snout to the origins of the first (Fig. 13) and second dorsal fins, the lengths of the caudal peduncle, anal fin base, pectoral fins, head (Fig. 11) and mandible (Fig. 12). The species also has black on the first and second dorsals, anal and pelvic fins and large teeth extending onto the lips of the upper and lower jaws.

The dentition and pigmentation patterns shared by *C. arge* and *M. crystallina* (Figs. 16C and D) are unique in *Chirostoma*. Although the former character has varied during the evolution of the genus, the changes have been quantitative rather than qualitative (except for the appearance of vomerine teeth in *C. humboldtianum*, *C. estor estor* and *C. bartoni*). Striking pigmentation patterns have evolved only once in *C. promelas*. I interpret this character concordance as an indication of the close relationship between these species; it is unlikely that they evolved independently. This

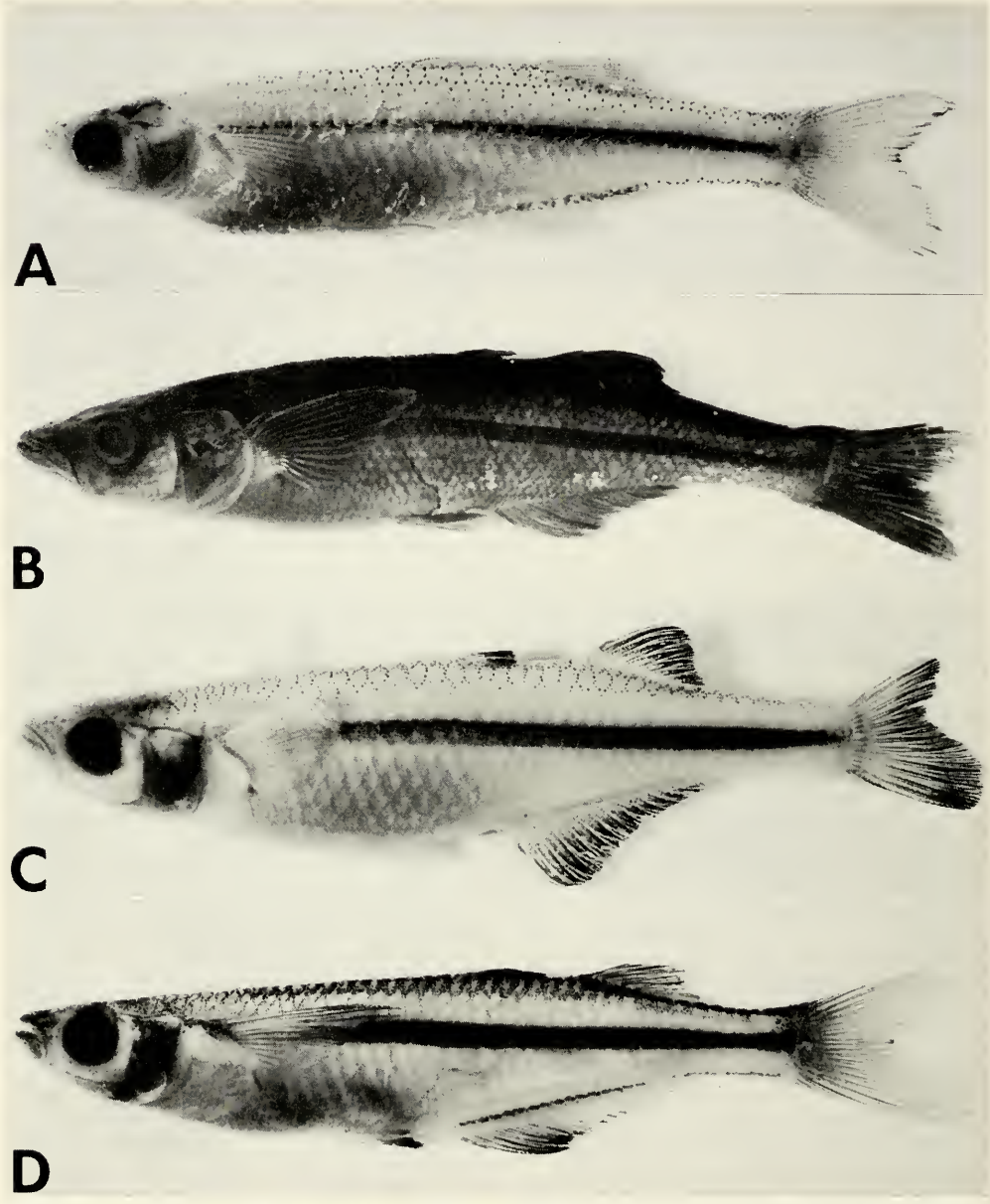


Figure 16. (A) *C. jordani*, UMMZ 197611, 52.8 mm S.L.; (B) *C. humboldtianum*, FMNH 73320, 148.6 mm S.L.; (C) *C. arge*, UMMZ 197622, 59.0 mm S.L.; (D) *Melaniris crystallina*, UMMZ 197605, 68.7 mm S.L.

relationship and the parallel morphological trends in the species groups of increasing body length and meristic and morphometric values suggest that *Chirostoma* is a phyletically unnatural assemblage of species.

There are two or perhaps three independent lines of evolution in *Chirostoma*. The most distinct lineage is the jordani group, which as a whole is the most widely distributed, contains the greatest number of species and is the most consistent in its patterns of variation. This group was prob-

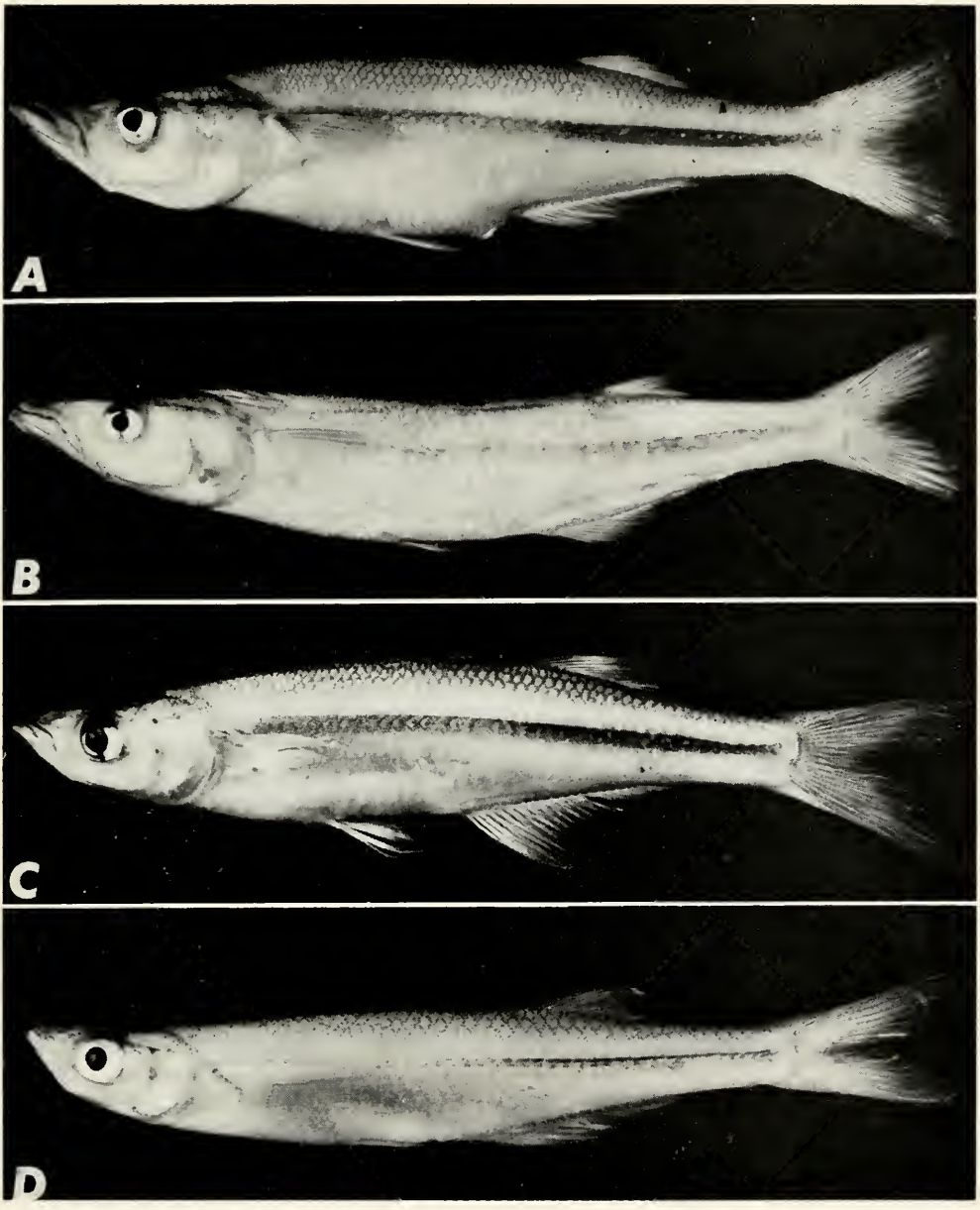


Figure 17. (A) *C. lucius*, UMMZ 197648, 228.3 mm S.L.; (B) *C. sphyraena*, 197647, 204.9 mm S.L.; (C) *C. consocium consocium*, TU 40845, 115.1 mm S.L.; (D) *C. chapalae*, TU 40836, 80.4 mm S.L.

ably the first to begin radiating on the Mesa Central, diverging early from a *Menidia*-like form (perhaps the ancestor of *M. berylina*). While the jordani group was differentiating in fresh water, the lineage leading to *Melaniris* and the arge group diverged from the *Menidia* ancestor evolving its distinctive dentition and pigmentation pattern. A subsequent split in this line led to an invasion of the Lerma-Santiago river system and the arge group on one hand and *Melaniris crystallina* on the other. The morphometric and

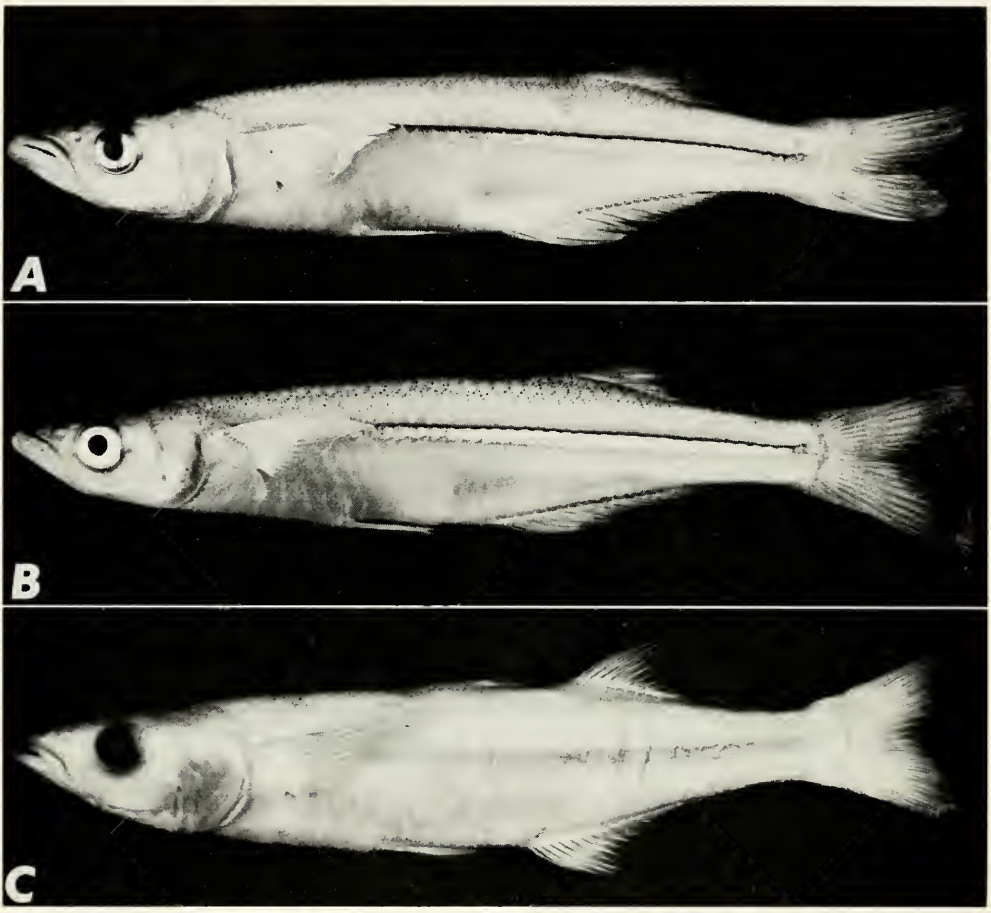


Figure 18. (A) *C. aculeatum*, holotype, TU 40889, 85.0 mm S.L.; (B) *C. labarcae*, TU 31958, 75.9 mm S.L.; *C. consocium reseratum*, UMMZ 197642, 168.1 mm S.L.

meristic specializations characteristic of *M. crystallina* probably appeared after this division.

As described above, pores and canals appear in the scales of the lateral line systems of *Menidia berylina* and *Melaniris crystallina*. The type of opening in the scales of the ancestral species is unknown, but appears to be irrelevant to the course of evolution of this character once the species had invaded the fresh waters of central Mexico. *C. arge* and *C. jordani* have lateral line scales with canals or pores on the same individuals, although in the former species, this condition is restricted to populations in the Río de la Laja. In the other members of the jordani species group, pores have been almost completely replaced by canals; they appear infrequently in only *C. patzcuaro*, *C. humboldtianum* and *C. grandocule*. In the remaining species of the arge group only pores are found, except for *C. labarcae* and *C. aculeatum*. These two species have lateral line scales with canals. The selection pressure responsible for this trend of replacement of pores is not known although it may be related to habitat. Almost all of the species with scale canals have probably evolved or lived for a long time in a lacustrine environment, whereas most of those with pores either live in streams or are recently derived from stream forms.

An alternative hypothesis for the origin of the arge group is the argument that most of the species evolved from a *Melaniris*-like ancestor (similar to *C. riojai*) before the

origin of canals in the lateral line scales and the characteristic pigmentation and dentition patterns and that *C. arge* represents a third, later arrival. Although this scheme eliminates the need for the reversal of these characters, I consider it unnecessary. The variation in *C. jordani* and *C. arge* suggests that the characters may have become unstable and variable when the ancestors first invaded fresh water. In this situation reversals would not be difficult.

The hypothesis that *Chirostoma* is monophyletic and that *M. crystallina* is an offshoot of the arge group is considered to be unlikely.

Chirostoma is most likely diphyletic. A future revision of the Atherinidae will probably result in a breakup of the genus as it is now constituted, hopefully along the lines outlined above.

Evolution Within the Species Groups

The jordani species group.—C. jordani is probably a slightly differentiated version of the ancestral stock which originally invaded the Lerma-Santiago system. The first major step in the evolution of the jordani species was the differentiation of the ancestral *C. humboldtianum* from this stock. This transition was accompanied by a great increase in size (from average of about 70–80 mm S.L. to around 200 mm S.L.) and an increase in the number of scales, fin rays, gill rakers and vertebrae. Canals tended to replace pores in the lateral line and the scale margins became laciniate. Morphometrically, the values of the two species overlap considerably, but there seems to have been a relative decrease in eye length, length of the anal fin base and pelvic fins and in the height of the anal and second dorsal fins. A relative increase in the length of the snout, mandible and head and in the distance between the snout and the origins of the pelvic and anal fins can also be detected.

Two species fall between *C. jordani* and *C. humboldtianum. C. patzcuaro*, a small species, has an occasional pore in its lateral line and a slightly pointed snout. Its meristic values fall within the range of *C. humboldtianum*, and its predorsal scales are slightly crowded and irregular in some specimens. The apparent close relationship between *C. patzcuaro* and the nominal *C. regani* has been discussed. *C. regani* may represent a level of evolution just ancestral to *C. humboldtianum* and *C. patzcuaro* an offshoot from this stock.

The second species, *C. chapalae*, shares with *C. jordani* a small, oblique mouth, a short head, postorbital distance and snout length and a faint concentration of melanophores along the posterior margin of the caudal fin. Meristically, it is within the range of *C. humboldtianum*, but lacks the higher numbers of predorsal scales. Because of these differences and the pigmentation pattern, I feel that *C. chapalae* also diverged just prior to *C. humboldtianum.*

C. humboldtianum, existing now as relict population, probably ranged more or less continuously from the Valley of Mexico to western Jalisco and Nayarit at various times in the past. The remaining members of the jordani group probably evolved from isolated populations of this species. One lineage leads directly to *C. consocium.* The evolution of this species will be discussed in more detail elsewhere. Suffice it to say here that it is the closest relative to *C. humboldtianum* that exists in the Lake Chapala area.

A second line leads to *C. estor.* This species differs primarily by having a longer body and higher number of median lateral and predorsal scales. It has not evolved any unique trophic structures except for occasional teeth on the vomer.

A third line leads from the *humboldtianum* ancestor to *C. grandocule.* This species still retains an occasional pore in the lateral line scales and has diverged primarily in its exceptionally high number of gill rakers (Fig. 9).

The fourth lineage leads to *C. lucius*, *C. sphyraena* and *C. promelas.* I have assumed this line to be independent of the others, but there is a possibility that these species may have derived their high scale counts from the ancestor to *C. estor.* The increase in the values of these characters in the western populations of *C. humboldtianum* suggests that it can occur independently. The length of the lower jaw has diverged in these three species. In *C. sphyraena* it usually projects little beyond the slender snout whereas in *C. lucius* it may project far beyond a broad snout. In *C. promelas* the lower jaw is shorter and included by the snout. These species are the most derived in the jordani species group.

These relationships are shown in the right hand branch of the phylogeny illustrated in Figure 15.

The arge species group.—The major event in the evolution of the arge group was the isolation and differentiation of populations of the *Melaniris*-like ancestor. There is no generalized species directly comparable to *C. humboldtianum* in the arge group. *C. arge* still partially retains specialized ancestral characters lost in all other species.

The line leading to *C. labarcae* and *C. aculeatum* probably diverged early. Both of these species have pointed snouts, moderately large to large teeth, lateral line scales with canals and an exceptionally high number of anal fin rays.

Three other populations have diverged in a different direction. *C. attenuatum attenuatum* shows an increase in body size and number of gill rakers and *C. a. zirahuen* has developed a very high number of median lateral scales (Fig. 5). *C. bartoni*, on the other hand, has only a slightly higher number of predorsal scales, anal fin rays and gill rakers, but has a more angular snout and occasionally teeth on the vomer.

A third cluster of species seems to have diverged very little from isolated populations of a *C. arge*-like ancestor. *C. melanoccus* differs primarily by having very small teeth and a higher number of gill rakers (Fig. 9). *C. riojai* and *C. charari* differ by having higher anal fins (Fig. 14). The latter species has fewer and smaller teeth and a more anterior placement of the dorsal fins (Fig. 13); the former has larger eyes, a greater postorbital distance and more anteriorly projecting premaxillaries. All have lateral line scales with pores.

The left hand branch of the phylogeny shown in Fig. 15 summarizes the above discussion and considers *Melaniris* to be an offshoot of the line leading to the arge group as a whole. An alternative view of the origin of the four species discussed immediately above is that the *arge* ancestor split into two populations which gave rise to the predecessor of *C. arge* and *C. melanoccus* on one hand and *C. riojai* and *C. charari* on the other. Each of these lineages subsequently divided resulting in the four existing species.

Poorly defined morphological trends, generally low morphometric and meristic values, reversals, and abrupt increases in certain meristic characters (median lateral scales, anal fin rays and gill rakers) suggest that the arge species group is evolving parallel to the jordani group but behind it in time. Similar events must have occurred after the jordani ancestor invaded the Lerma-Santiago river system. A small species, it was preadapted to survive in streams and later successfully entered lacustrine environments. This shift in habitats was accompanied by an increase in body size and most body proportions and an increase in the number of scales, fin rays, gill rakers and vertebrae. Superimposed on these trends are a few specific trophic specializations. It is this view of the evolution of *Chirostoma* which resulted in the arrangement of the species in the figures. This is not an artificial clustering of ecospecies along morphological gradients. It is a reflection of the evolutionary events that can occur when a species enters a relatively open environment and undergoes phyletic differentiation as well as adaptive radiation. There are few critical gaps in the morphological record presented by the existing species. Thus, it is fairly easy to see the direction that evolution has taken and where the morphoclines (Maslin, 1952) have been modified.

Conclusions

1. The genus *Chirostoma* consists of eighteen species and six subspecies not including *C. compressum*, thought to be extinct.

2. Primitive versus derived character states for *Chirostoma* are considered to be, respectively: smooth versus laciniate scale margins, pores versus canals in the lateral line scales, small teeth placed within the gape on the dentaries and premaxillaries versus large teeth so placed or small or large teeth in any other location, low range versus high range of meristic values. Extreme morphometric values in any direction and distinctive patterns of pigmentation are also considered derived.

3. *Chirostoma* is separable into two species groups on the basis of meristic characters and scale morphology. The jordani group tends to have a high range of meristic values, laciniate scales with lateral line canals; the arge group, with few exceptions, has a low

range of meristic values, smooth-edged scales and lateral line pores.

4. *C. jordani* is considered to be the most primitive member of the jordani species group and *C. arge*, *C. melanoccus* and *C. riojai* the most primitive members of the arge species group. However, *C. arge* closely resembles *Melaniris crystallina* in pigmentation pattern and dentition and is considered, in spite of its specializations, closest to the ancestral stock of the arge species group.

5. *Chirostoma* is most likely diphyletic. The jordani species group diverged from a *Menidia*-like species which invaded the Lerma-Santiago river system very early. The arge species group evolved from a *Melaniris*-like stock which invaded the same basin at a later time.

6. Both species groups show trends of replacement of primitive character states by those considered to be derived. The arge species group seems, however, to be at an earlier stage of this process.

7. The most important step in the evolution of the jordani species group was the appearance of a large, generalized species probably very similar to the eastern populations of *C. humboldtianum*. This widespread form seems to have given rise to most of the other members of the species group.

8. The arge species group seems to have evolved from populations of a species similar to *C. arge* and *Melaniris crystallina*. No generalized species comparable to *C. humboldtianum* exists in this group.

Resumen

1. El Género *Chirostoma* consiste de 18 especies y 6 subespecies, sin incluir *C. compressum* De Buen, que se considera está extinguido. Los siguientes nombres en uso corriente se sinonimizan aqui: *Otalia* = *Christoma*; *C. ocampoi* y *C. regani* = *C. humboldtianum*; *C. diazi* = *C. sphyraena*; *C. ocotlanae* = *C. lucius*. No se reconocen subespecies de *C. jordani*. *C. reseratum* se refiere a *C. consocium* a nivel subespecifico. El nombre *C. attenuatum* Meek es revalidado para las poblaciones de los Lagos de Pátzcuaro y Zirahuén, a la fecha designados como *C. bartoni*. Cinco ejemplares del lago que está junto al Balneario de Cointzio, Michoacán, son referidos a *C. charari* De Buen. No se designa neotipo debido al pequeno numero de ejemplares. *C. aculeatum* se describe como nuevo.

2. Estados primitivos versus derivados para caracteristicas de *Chirostoma* se considera son, respectivamente: bordes de las escamas lisos versus laciniados, poros versus canales en la línea lateral, dientes pequeños colocados dentro de la cavidad sobre los dentarios y premaxilares versus dientes grandes colocados igual o dientes pequenos o grandes en cualquier otra posición, números altos de variacion merística versus números bajos. Valores morfométricos extremos en cualquier dirección y patrones distintivos de pigmentación se consideran también derivados.

3. *Chirostoma* es separable en dos grupos de especies sobre la base de características merísticas y morfología de las escamas. El grupo jordani tiende a tener el número alto de valores merísticos, escamas laciniadas con canales en la línea lateral; el grupo arge tiene número baja de los valores merísticos, bordes de las escamas lisos y poros en la línea lateral.

4. *C. jordani* se considera el miembro mas primitivo del grupo de especies jordani y *C. arge*, *C. melanoccus* y *C. riojai* los miembros mas primitivos del grupo de especies arge. Sin embargo, *C. arge* se parece estrechamente a *Melaniris crystallina* en patrón de pigmentacion y dentición, y es considerado, a pesar de sus especializaciones, mas cercano a la forma ancestral del grupo de especies arge.

5. *Chirostoma* es mas probablemente difilético. El grupo de especies jordani divergió de una especie semejante a *Menidia* que invadió el sistema fluvial Lerma-Santiago muy temprano. El grupo de especies arge evolucionó de una entidad semejante a *Melaniris* que invadió la misma cuenca en un tiempo posterior.

6. Ambos grupos de especies muestran tendencias de reemplazo de estados primitivos de características por aquellos que se consideran derivados. El grupo de especies arge parece, sin embargo, estar en una etapa mas temprana de este proceso.

7. El paso mas importante en la evolución del grupo de especies jordani fue la aparición de una especie grande, generalizada, probablemente muy similar a las poblaciones orientales de *C. humboldtianum*. Esta forma ampliamente distribuída parece haber dado lugar a la mayoría de los otros miembros del grupo de especies.

8. El grupo de especies arge parece haber evolucionado de poblaciones de una especies similar a *C. arge*. No existe ninguna especie generalizada comparable a *C. humboldtianum* an este grupo.

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A NEW SPECIES OF MAP TURTLE (GENUS *GRAPTEMYS*) FROM THE GUADALUPE RIVER SYSTEM IN TEXAS

DAVID HAYNES
The University of Texas Institute of Texas Cultures at San Antonio, P.O. Box 1226, San Antonio, Texas 78294
and
RONALD R. McKOWN
Department of Biology, West Texas State University, Canyon, Texas 79015 p. 143

AN ECOLOGICAL STUDY OF THE QUEEN SNAKE, *REGINA SEPTEMVITTATA* (SAY) IN KENTUCKY

BRANLEY A. BRANSON and EDD C. BAKER
Eastern Kentucky University, Richmond, Kentucky 40475 p. 153

ETHEOSTOMA BOSCHUNGI, A NEW PERCID FISH FROM THE TENNESSEE RIVER DRAINAGE IN NORTHERN ALABAMA AND WESTERN TENNESSEE

BENJAMIN R. WALL, JR.
Biology Department, Walker College, Jasper, Alabama 35501
and
JAMES D. WILLIAMS
Biology Department, Tuskegee Institute, Tuskegee Institute, Alabama 36088 p. 172

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A NEW SPECIES OF MAP TURTLE (GENUS *GRAPTEMYS*) FROM THE GUADALUPE RIVER SYSTEM IN TEXAS

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ABSTRACT

A map turtle of the genus *Graptemys*, from the Guadalupe–San Antonio River system of Texas, is described as a new species. Notes on reproduction, feeding habits, and habitat are included; the range and presumed relationships with other members of the genus are discussed.

Several specimens of an undescribed species of *Graptemys* have been collected in the Guadalupe River system in recent years. These were thought at first to be variants of either *Graptemys versa* Stejneger, which occurs in the Colorado River system in Texas (Olson, 1959; Webb, 1962), or of *Graptemys pseudogeographica* (Gray), which is known from the Red, Sabine, and Neches rivers of northern and eastern Texas (Raun, 1959). Field work that we undertook during the spring, summer, and fall of 1967 and the spring of 1968 in the Guadalupe River system yielded 66 additional specimens of *Graptemys*. Studies on the morphology of these turtles and comparison with examples of previously known Texas *Graptemys*, have led us to conclude that they represent an undescribed allopatric species distinct from *G. versa*, its closest geographical relative. The facts that the Guadalupe River and the Colorado River have probably been separated from each other since at least the late Pleistocene and that morphological differences between the populations are greater than between subspecies in other members of the genus support this conclusion. Collection of these turtles extends the known range of the genus *Graptemys* almost one hundred miles southwest of the Colorado River, which previously was the southwesternmost stream system from which map turtles were known (Fig. 1). There are smaller rivers and tributaries in the intervening 100 miles, but no intermediate forms have been found between these turtles and *G. versa*, nor is there any evidence of overlap in the ranges of these two species. Information on reproductive isolation is not available at this time, and there is no evidence that this species interbreeds with any other form of *Graptemys*, all of which are now geographically isolated from it. We name it in memory of Fred R. Cagle whose research greatly increased our knowledge of *Graptemys* and turtles of the southern states in general.

The abbreviations used in the descriptions are: Cl = carapace length, Cw = carapace width, Pl = plastron length, Pw = plastron width, Hw = head width, Ht = height, and Aw = alveolar width. All measurements are maximum. All specimens have been deposited in the Texas Natural History Collection, Austin, Texas. All color descriptions in the text are from preserved specimens.

Graptemys ***caglei*** new species

Fig. 2

Holotype: TNHC 36061, an adult male, from the Guadalupe River, 8 km NW Cuero, DeWitt Co., Texas, 29 June 1967.

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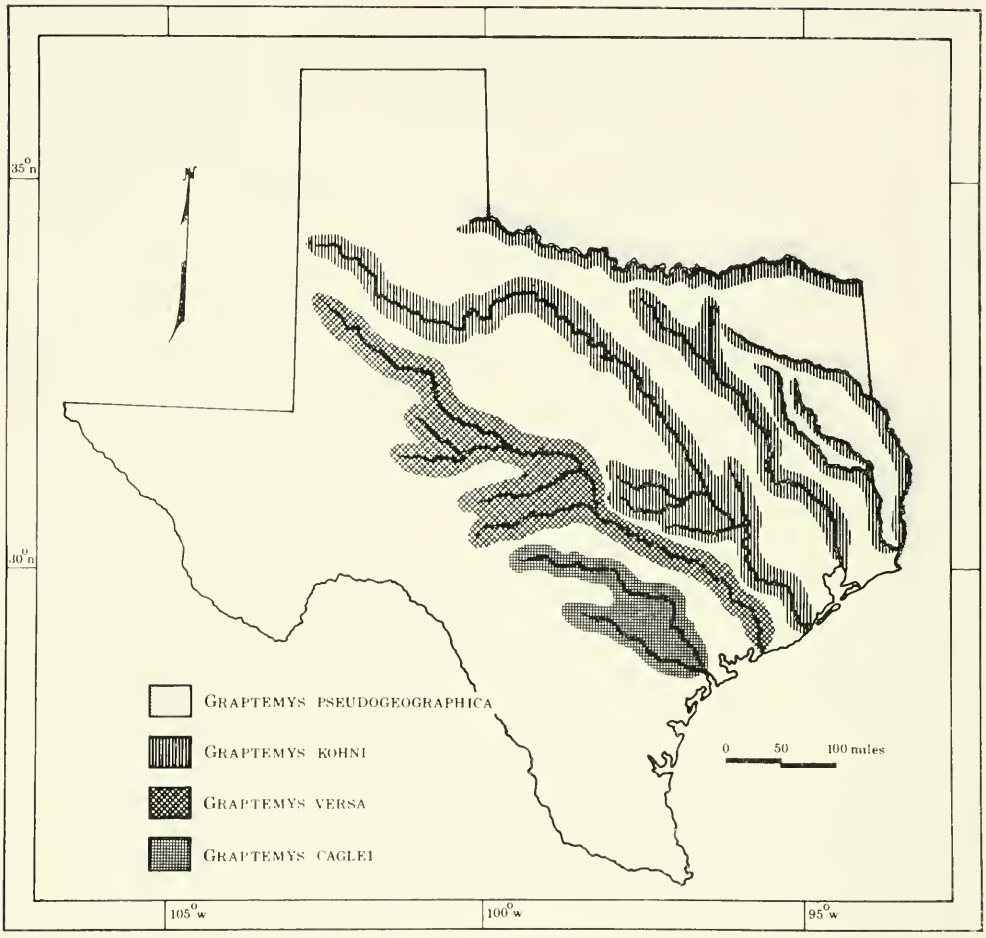

Figure 1. Texas river systems in which turtles of the genus *Graptemys* are known to occur: *G. pseudogeographica* (Red, Sabine, and Neches rivers of northern and eastern Texas); *G. kohni* (Red, Sabine, Neches, Trinity, and Brazos rivers of eastern and central Texas); *G. versa* (Colorado River system of central Texas); and *G. caglei* (Guadalupe–San Antonio River system of south central Texas). The map shows only the river systems. It does not indicate the actual ranges of the various species, which, on the basis of current knowledge, are known only from several to many collecting stations in each system.

Paratypes: The paratypic series consists of five juveniles (TNHC 36056, 36077, 36080–36082), one subadult female (TNHC 76103), 33 adult males (TNHC 36068–36070, 36072, 36074–36076, 36078–36079, 36083–36091, 36093–36098, 36100–36102, 36104–36109), and one adult female (TNHC 41223). We collected all of these specimens at the type locality during the fall of 1967 and the spring of 1968 except for 36106 and 41223 which were taken 12 km SW Hunt, Kerr Co., Texas. All specimens are preserved in formalin except for 36104–36109, which are skeletons.

Diagnosis: A species of *Graptemys* most closely resembling *G. versa*, but differing from the latter and others in having the following combination of characteristics: (1) ventral surface of jaw with a transverse cream-colored line (Fig. 3); (2) dorsal head pattern with a light "V"–shaped mark (Fig. 4); (3) plane of top of head toward snout horizontal in profile, snout somewhat pointed (Fig. 5); (4) low vertebral spines, pos-

terior midline of vertebrals brown or black; (5) carapace somewhat flattened and with central portions of scutes raised above their borders; (6) carapace predominately green in coloration; (7) tendency toward black flecking on plastron of adult males (Fig. 3); (8) supraoccipital spine short, expanded dorso-ventrally (Fig. 6); and (9) adult females do not develop wide heads or broadened alveolar surfaces.

Description of Holotype: TNHC 36061 is a medium-sized adult male with the following measurements: Cl, 9.00 cm; Cw (at juncture of fourth and fifth marginals), 5.97 cm; Cw (at juncture of seventh and eighth marginals), 7.05 cm; Pl, 7.58 cm; Pw (anterior to the inguinal scute), 5.08 cm; Ht (posterior to the spine of the second vertebral), 3.35 cm; Hw (at the anterior margin of the tympanum), 1.40 cm; Aw, 0.24 cm. Carapace elliptical in dorsal aspect, narrowed in front, sharply serrated posterior to the eighth marginals; shell moderately flattened in cross section (height of shell 47% of width at juncture of seventh and eighth marginals); middorsal keel well developed with prominent vertebral spines; lateral, anterior, and posterior margins slightly flared outward; centers of costal scutes raised (knobby) above borders of each scute.

Ground color of carapace light green; costal and marginal scutes with one or more roughly circular cream-colored lines, centers of circular markings with alternating circles of black and green lines of a lesser thickness than the cream-colored lines; vertebral spines brown- or black-tipped.

Plastron slightly rounded in front; slight ventral flare at lateral margins of femoral scutes; dorsal flare at anterior of humeral scutes; shallow anal notch; plane of plastron 0.75 cm below plane through edge of fifth to seventh marginals.

Ground color of plastron pale cream-colored with faded black markings extending along borders of each plastral scute; black coloration varies from thin lines (0.34 cm) along borders of anterior scutes to thicker blotches (0.92 cm) along borders of posterior scutes; cream-colored portion of plastral scutes with black flecks; bridge with four black, longitudinal, wavy lines; and four black wavy lines on the ventral surface of the fifth to eighth marginals.

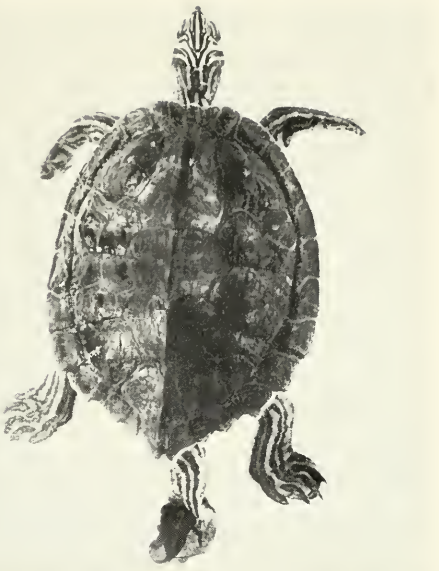

Figure 2. Type specimen of *Graptemys caglei* (TNHC 36061), an adult male (carapace length 9.00 cm), collected in the Guadalupe River, 8 km NW Cuero, DeWitt Co., Texas.

Ground color of head, neck, and distal portions of the limbs black; ground color cream-colored on the axillary and inguinal areas beneath the carapace; seven cream-colored stripes on dorsal surface of head, the center stripe the widest; one thin cream-colored line extends laterally and ventrally from the nostrils beneath the orbit to the non-pigmented portion of jaw; one wide cream-colored line extends as a transverse line onto ventral horny surface of lower jaw; a series of five black lines form circular and rectangular markings on ventral surface of neck; first cream-colored line posterior to orbit extends from below each orbit dorsally and posteriorly and meets its partner from the opposite side of the head at a point in the midline approximately one cm behind orbits; five additional cream-colored lines extend similarly but do not meet at midline; 22 more or less continuous cream-colored lines extend along neck posterior to the region of the fore limbs where cream becomes the dominant color. Three cream-colored lines extend from under carapace to the claws on anterior dorsal surface of fore feet; three additional inter-

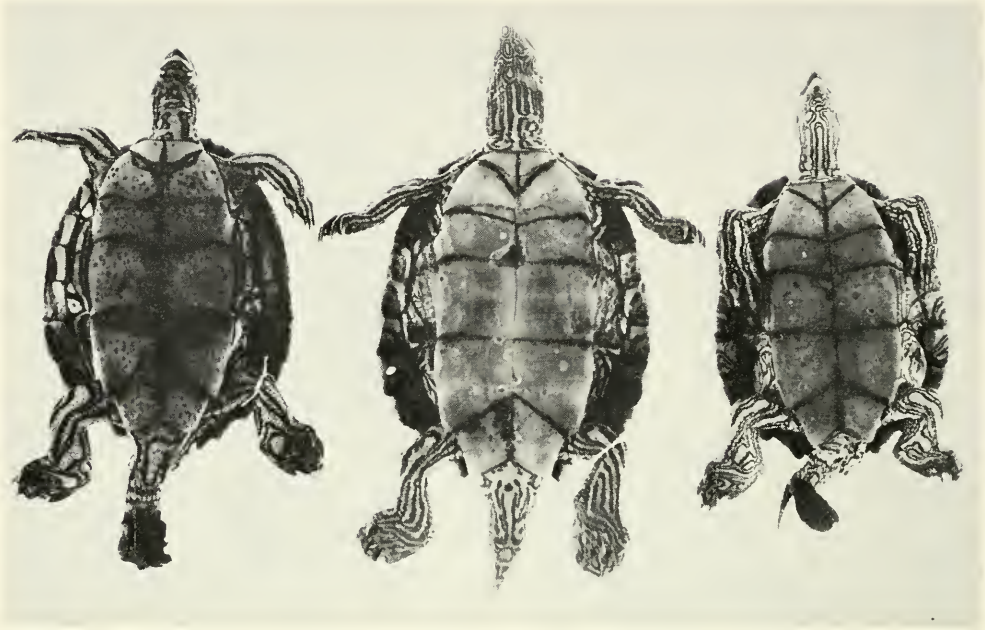

Figure 3. Comparison of the ventral surfaces of adult males: *G. caglei* (left), *G. kohni* (center), and *G. versa* (right). Note the black flecks on the plastron of *G. caglei* and the differences in chin patterns.

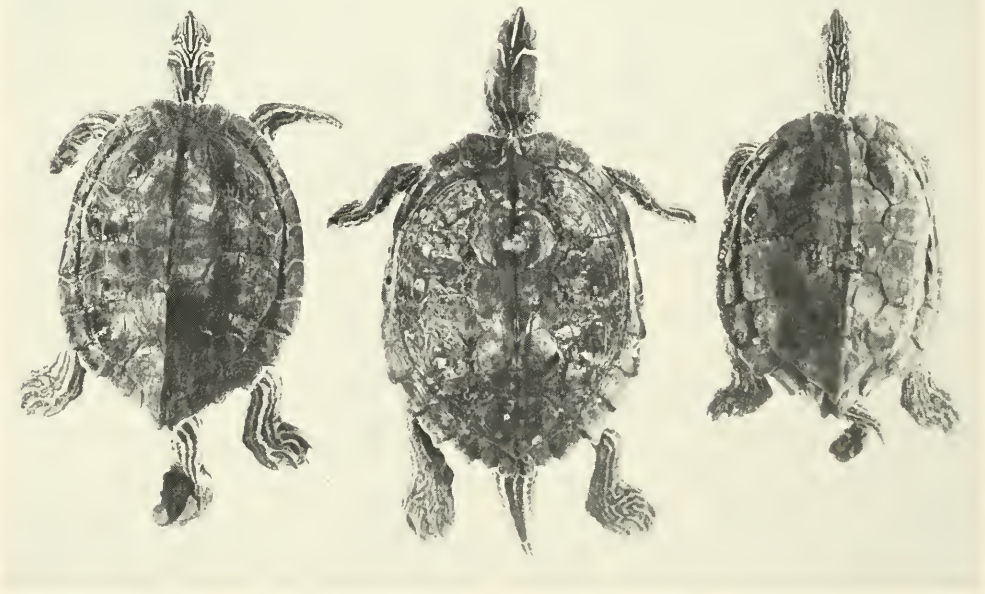

Figure 4. Dorsal view of adult males: *G. caglei* (left), *G. kohni* (center), and *G. versa* (right). The head pattern and coloration of the vertebral spines are similar in *caglei* and *kohni*.

Figure 5. Lateral view of adult males: *G. caglei* (top left), *G. kohni* (bottom left), and *G. versa* (right). The light postorbital line in *caglei* and *kohni* originates beneath the orbit and continues onto the dorsal surface of the head, whereas in *versa* the postorbital line forms a letter "J" on the lateral surface of the head.

Figure 6. Skulls of adult females: *G. caglei* (left), *G. kohni* (center), and *G. versa* (right). Note the differences in the length and dorso-ventral expansion of the supraoccipital spine.

spersed lines extend similarly on fore feet without reaching claws; four cream-colored lines from axillary region break eventually into rectangular and circular markings near and on posterior surface of fore feet. Ten cream-colored lines extend the length of hind limbs, three of these on dorsal surface reach the claws; 15 cream-colored lines extend onto the tail for various distances, one line on each side reaching tip of tail.

Description of Paratypes: The 40 turtles of the paratypic series are described according to age and sex.

Juveniles. The coloration and pattern of the soft parts and carapace of the five juveniles are similar to those of the holotype. Slight variations exist in the number and length of the lines on the soft parts, but the color is consistent. The series ranges in plastron length from 4.23 cm to 6.41 cm. Since the smallest mature male (determined mature by dissection) has a plastron length

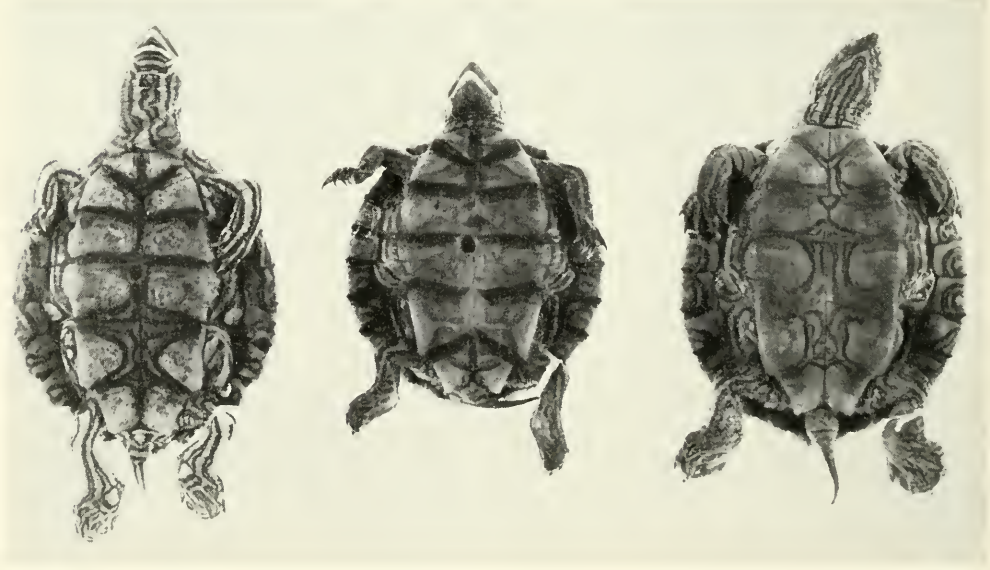

Figure 7. Ventral surfaces of juveniles: *G. caglei* (left), *G. kohni* (center), and *G. versa* (right). Juvenile *caglei* lack the black plastral flecks that characterize adult males.

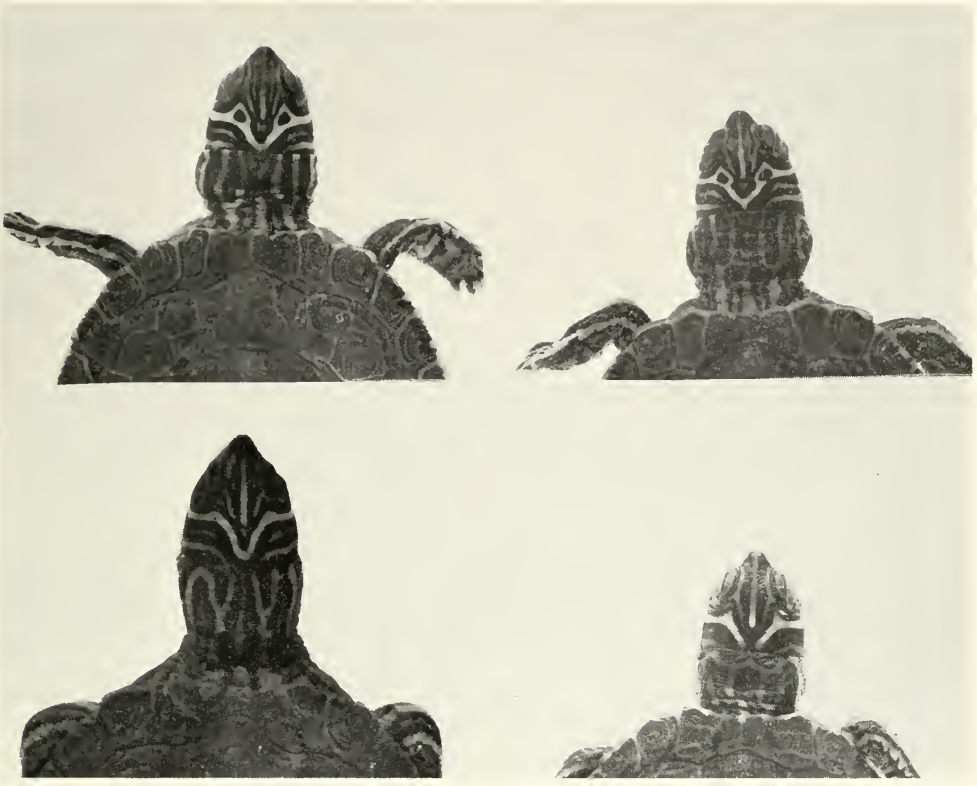

Figure 8. Variation in the head pattern of four juveniles of *G. caglei*. In eight of the 67 specimens available for study, the broad light lines of the head pattern fail to meet in the characteristic "V" (as shown at bottom right).

of 6.18 cm, three larger specimens in the juvenile series (6.20, 6.29, and 6.41 cm) were judged to be juvenile females.

The color pattern of the plastron differs from that of the holotype in that the dark lines are thicker and bolder, and the juveniles (Fig. 7) lack the black flecks that are characteristic of adult males (Fig. 3). In one specimen the lines do not meet to form the "V" on the dorsal surface of the neck as in the holotype, but they approach each other near the midline and extend posteriorly to the carapace (see Fig. 8 for pattern variations). Like other juvenile *Graptemys*, the specimens are almost round—Cl/Cw approaches 1.00. The smallest specimens are slightly larger than hatchlings; all show evidence of growth zones.

Adult Males. The 33 adult males are similar to the holotype, but there is some variability in the number and length of the lines on the soft parts. These males range in plastron length from 6.18 cm to 9.28 cm. In two specimens the lines on the posterodorsal surface of the head fail to meet in a "V", but they approach each other and then extend posteriorly.

Adult Females. The two females (one adult and one subadult) are similar to the males in coloration and pattern, but their shells are more rounded. They also have lower vertebral spines. The fully adult specimen has Pl, 14.55 cm; Cl, 16.11 cm; Cw, 12.17 cm; Hw, 2.55 cm. Larger adult females were observed in the Guadalupe River.

Range: The Guadalupe–San Antonio River system of south central Texas. Specimens have been collected or observed at the following localities: *Guadalupe River*, DeWitt Co., 8 km NW Cuero at Texas highway 766 (type locality); Gonzales Co., 1 km S Gonzales; Kerr Co., 12 km SW Hunt; *Blanco River*, Hays Co.; 15 km NW San Marcos; *San Marcos River*, Gonzales Co.,

Palmetto State Park. Intensive search has failed to provide material from adjacent river systems. We assume, therefore, that the species is confined to one river system just as several other species of *Graptemys* are restricted to single systems (Cagle, 1953, 1954).

G. caglei is abundant at the type locality and in other sections of the Guadalupe River, the San Antonio River, and several smaller tributaries. In some parts of the rivers this may be the dominant species of turtle.

Food Habits: The stomach contents of several juveniles and adult males and two subadult females were examined for food items and parasites. All were collected in July and all contained large amounts of food consisting of both plant and animal material. Most of the plant matter, however, was bark from decomposing twigs, algae, and fragments of grass such as are found on the larval cases of caddis flies (Tricoptera). Most of the plant material was probably ingested incidental to feeding upon insects or snails.

Juvenile turtles contained considerable amounts of bark and pieces of grasses embedded in larval caddis fly cases. Small gnat-like dipteran insects were also present in considerable numbers. The large concentration of these minute insects suggests that they were probably ingested dead after being washed against twigs or other items at the water's surface. The only food items found in the stomachs of adult males were caddis fly larvae and larval cases. Some algae and grass were also present, probably as constituents of the caddis fly cases. Food items in the subadult females were essentially the same as those for the adult males, except that small fragments of small, thin-shelled gastropods were also included. Although different food items are certainly utilized at different seasons of the year, insects probably constitute the basic food of this turtle.

Reproduction: Hatchling turtles have been observed and collected from September through November, which indicates a late spring to early summer nesting period. Sand bars are essentially absent in many parts of the Guadalupe River, and the nesting habits may be different from those of many other species of *Graptemys*.

Habitat: The Guadalupe River rises on the Edwards Plateau in the Balconian Biotic Province (Blair, 1950), flows southeastward and across the Balcones Escarpment into the Texan Biotic Province and to the Gulf of Mexico. Much of the river bottom on the Edwards Plateau is limestone. The river in that area has a wide bed (50 to 70 meters) and carries a relatively small volume of water with a moderate current. Long stretches of shallow water connect small pools from one to three meters deep. Along the shallow stretches, the river has carved numerous narrow channels that vary from less than one-half to more than a meter deep. Many small dams impound pools or small lakes that may approach two meters in depth. *Graptemys* have been found basking on rocks in the shallow stretches and on logs and cypress knees in the pools and impoundments.

The character of the river changes as it passes into the Texan Biotic Province. It becomes generally deeper and muddier and not so rapid. The river at the type locality averages two to three meters deep and about 12 to 25 meters wide. Most of the turtles were collected from this area because it is easily accessible and can be traversed with a motor boat. At the type locality, turtles were found basking during the day on logs and brush above some of the deeper holes. Logs that had fallen into the river and maintained a connection with the bank were shunned as basking spots.

Graptemys caglei has been infrequently collected in the San Marcos River. Intensive collecting of both the San Antonio and Medina Rivers has yielded only a few sight records.

Discussion of Evolutionary Relationships: Graptemys caglei appears to be closely related to both *G. versa* and *G. kohni* (Baur). The osteology of equivalent-sized individuals of the three species shows some differences in the skulls of females (Fig. 6). Females of *G. kohni*, however, are known to reach a much greater size than those of either *G. versa* or *G. caglei*, and they have greater alveolar width. Extremely large females of *G. kohni* have head widths approaching the head widths found in *G. pulchra* Baur and *G. barbouri* Carr and Marchand.

The head patterns of *G. caglei* closely resemble those of *G. kohni* (Figs. 4 and 5), but the evolutionary implications of head patterns are unknown, except that, within limits, those of closely related *Graptemys*

Table 1. Comparison of Related Texas *Graptemys*.

Graptemys versa	*Graptemys caglei*	*Graptemys kohni*
Ventral surface of jaw with longitudinal orange mark at symphysis.	Ventral surface of jaw with transverse cream-colored line (Fig. 3).	Ventral surface of jaw with longitudinal yellow mark at symphysis.
Head pattern with "J"-shaped mark.	Head pattern with "V"-shaped mark (Fig. 4).	Head pattern with "V"-shaped mark.
Plane of top of head toward snout somewhat rounded downward.	Plane of top of head toward snout horizontal; snout somewhat pointed (Fig. 5).	Plane of top of head toward snout horizontal; snout somewhat pointed.
Low vertebral spines (posterior part of each vertebral elevated above adjacent vertebral); posterior midline of vertebrals horn-colored.	Medium vertebral spines; posterior midline of vertebrals brown or black.	High vertebral spines; spines black-tipped.
Carapace somewhat flattened and knobby.	Carapace somewhat flattened and knobby.	Carapace neither flattened nor knobby.
Carapace predominantly olive.	Carapace predominantly green.	Carapace predominantly brownish with black marks on costals and some marginals (variable).
Adult females do not develop wide heads or broadened alveolar surfaces.	Adult females do not develop wide heads or broadened alveolar surfaces.	Adult females develop wide heads and broadened alveolar surfaces.
Supraoccipital spine of medium length; not expanded dorso-ventrally.	Supraoccipital spine short; expanded dorso-ventrally (Fig. 6).	Supraoccipital spine long; not expanded dorso-ventrally.

are remarkably similar. The external morphology of the head of *G. caglei* is closer to that of *G. kohni* in that both are nearly flat across the top of the head from the nostrils to the posterior part of the skull. *G. versa* males have a rounded appearance from between the orbits to the nostrils as is also the case in *G. pseudogeographica* (Fig. 5). Comparisons among *G. caglei*, *G. versa*, and *G. kohni* are listed in Table 1.

In our opinion, *G. caglei* is a morphological intermediate between the narrow-headed *G. versa* and the broad-headed *G. kohni*.

Additional Specimens of G. caglei Examined: (26 specimens) TNHC 23053, 34022, 34023, 36054, 36055, 36057–36060, 36062–36067, 36071, 36099, 36621–36629 from various localities in the Guadalupe–San Antonio River system all collected by us except 23053, by Gerald Raun.

Comparative Materials Examined: (a total of 135 specimens). *G. versa* (91 specimens): TNHC 20478, 20479, 28631, 28648, 28654, 28659, 28660, 28663, 32917, and 34249 from the Colorado River system by various collectors, including 66 specimens from the Colorado River in Bastrop Co. and 15 from the Colorado River in Runnels Co., by us. *G. kohni* (44 specimens): 4 from the Sabine River in Gregg Co.; 2 specimens from the Neches River in Jasper-Hardin Cos.; 29 from the Trinity River in Trinity and Liberty Cos.; 2 from the Navasota River in Brazos-Grimes Cos.; all in Texas; 2 from the Mountain Fork River in McCurtain Co., Oklahoma; and 5 from the Little Missouri River in Pike Co., Arkansas, all by us.

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AN ECOLOGICAL STUDY OF THE QUEEN SNAKE, *REGINA SEPTEMVITTATA* (SAY) IN KENTUCKY

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ABSTRACT

The bulk of Kentucky queen snakes' diet (93.2%) consists of softshelled *Orconectes juvenilis*; the remainder is occasional fishes, tadpoles and other genera of crayfish. Food habits varied little between areas and between different times of the year. The snake is an opportunistic feeder, preying upon the most abundant crayfish in its habitat, taking prey by ambush.

The observed sex ratio, both in adults and newborn, was 1:1. Females generally do not reproduce until their third year, but immature eggs may be found during the second year in the ovaries, possibly being produced late in the fall of the first year. The minimum size of a mature female was 344 mm total length. Males become sexually mature during their second year. Mating probably occurs both in spring and fall, with young females mating for the first time during the second fall of life or the spring of the third year. Female snakes contained from 7 to 49 immature eggs in addition to mature eggs or embryos, representing the reproductive potential for the following season. This indicates an annual reproductive season rather than a biannual one. The total egg count increases proportionally with body size. Being viviparous, the retained eggs lack shells at all stages of development. The thin chorionic membrane of oviducal eggs lies in intimate contact with the maternal tissues during development. A notable increase in egg size during this time indicates transmission of dissolved nutrients. The number of young per litter varies between 8 to 17, averaging 12.8 per female. A discussion of the process of birth is presented. All newborn snakes shed their fetal, very thin, skin within 24 hours of parturition, and a thicker skin is shed four days later.

Growth rates were highest during the first year, yearlings showing an average increase of 75% length increase over newborn. The percentage increase for the second year class averaged 44.8. The total growth for specimens older than two years, regardless of age, was 14 to 15%.

Cloacal temperatures were higher by as much as 6.2° C than ambient ones, indicating a tendency toward temperature regulation. The mean cloacal temperature for all specimens was 25.6° C. The critical thermal maxima for adult queen snakes varied from 43.4° C to 44.5° C (mean, 43.9), whereas that of juveniles ranged from 39.5° to 41.5° (mean, 40.3), indicating that larger snakes have higher temperatures than juveniles, appearing to be proportional to body weight and length in the latter.

Comments upon hibernation, ectoparasites, homing, and population sizes are included.

INTRODUCTION

Few reports concerning the biology and ecology of the queen snake have been published, the literature generally being limited to check lists, field guides and handbooks. Only three short observations on *Regina septemvittata* in Kentucky have been published (Funkhouser, 1925; Barbour, 1968; Welter and Carr, 1939). The purpose of this report, then, is to present the results of our observations on certain aspects of the life history of Kentucky queen snakes, and to compare our ecological findings with reports from other areas. Our study ran from September, 1968 to September, 1969. During this period, we concentrated primarily upon food preferences, reproduction, temperature, home range and size variation, and habitat.

Based upon his field experiences in six states, Conant (1960) summarized the optimum habitat of *Regina septemvittata* as one of small to medium, permanent, relatively shallow streams with slight to moderate current, often with rocky banks and bottoms, usually in woodland surroundings. The species is normally absent from lakes and ponds

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and from mountain brooks and rills with heavy shade and high gradient. The habitat must be open enough for an abundance of sunshine for at least a few hours each clear day. The queen snake is not entirely confined to such habitats, however, for it is also found occasionally at the edge of marshes and in drainage canals and ditches. Wood's (1949) southwestern Ohio observations indicated that the rate of water current did not appear to have direct bearing on distribution, but that three conditions did appear necessary before large populations could develop: (1) permanent water areas, running or standing, where the water temperature remains at or above 65° F during most of the active season; (2) an abundance of cover, usually flat rocks lying partly in the water; and (3) an abundance of crayfish of the genus *Cambarus*.

Nakamura and Smith (1960) asserted that *Regina septemvittata*, as well as other members of the *Regina* group, are chemically cued to feed upon invertebrates. This observation was more or less corroborated by Burghardt's (1968) significant laboratory investigation on food and chemical preferences in young *Natrix sipedon*, *Regina grahami* and *R. septemvittata*. He found that *N. sipedon* preferred fish and amphibians, whereas *R. grahami* and *R. septemvittata* selected crayfish, especially newly molted *Cambarus*. However, many writers recognize that members of this group of snakes occasionally do eat vertebrates. Conant and Bridges (1939), for example, listed crayfish, fish and frogs in the queen snake's diet. Other items which have been reported from queen snake stomachs are: minnows (Minton, 1944); newts (Wright and Wright, 1957); mudminnows, snails of the genus *Physa*, and fairy shrimp (Adler and Tilley, 1960).

As concerns mating behavior and breeding habits, the literature is quite mute on *Regina septemvittata*, although there have been some reports on litter size and/or embryo counts (see below).

Materials and Methods

Food Preference and Feeding Habits. Food preferences of the queen snake were investigated by two methods: by tempting the snakes with various food items under laboratory conditions, and by dissection and examination of stomach contents of freshly captured specimens. Partially natural habitat conditions (excluding running water) were simulated by setting up two 15-gallon aquaria with natural creek gravel banked so that a portion remained above water level. A medium-sized flat rock was placed on the sand and partially submerged in the water to provide shelter for the snakes. These tanks were covered with full-aquarium hoods, lighted by fluorescent bulbs connected to a timer, by which a photoperiod was established (6:00 a.m. until 9:00 p.m.). The tanks were placed in a constant temperature room (27°) with no windows or other sources of light. During the photoperiod, the temperature reached 31° in the tanks because of heat given off by the light bulbs. A red 40-watt bulb was placed behind and slightly above each tank in order to facilitate post-photoperiod observations. The specimens were allowed to remain in the tanks for one week before food was offered in order to allow adjustment to the new habitat and to insure readiness to feed.

The food habits and preferences in nature were investigated by performing gut analyses of 120 specimens. This sample included 40 specimens captured in June, 40 in July, and 40 in August. In order to establish whether or not a preferred feeding time existed, some specimens were captured during the morning and some during the afternoon. The specimens were also taken at various stations to determine if feeding habits varied between populations. However, this was determined more by availability of specimens than by specific numbers at each station.

After measurements were taken in the field (see below), each specimen was decapitated and preserved in 10% formalin. Analyses of stomach, fore-gut and hind-gut contents were conducted in the laboratory.

Reproduction. The environmental set-up utilized for food preference observations was also used for the reproductive study. Ten gravid females, captured during July and the first two weeks of August, were placed in the aquaria and kept under the same photoperiod and temperature regimen as the specimens used for the food preference study until young were presented.

Body Temperature and Critical Thermal Maxima. Cloacal temperatures were determined for all specimens used in the study

by means of a Schultheis quick-recording reptile thermometer graduated to 0.1° C. Water and air temperatures at the point of capture of each specimen were taken and recorded on data sheets with the cloacal readings.

Specimens used for critical thermal maxima (CTM) determinations included ten adults and ten young-of-the-year without regard to size and sex. All twenty specimens were captured at Station I Tates Creek between the hours of 4:00 p.m. and 6:00 p.m., August 20, 1969, and removed immediately to the laboratory for testing. In order to determine the CTM of the species, and to compare that of the adult with that of juveniles, each specimen was measured, weighed, and measured for temperature. Each individual was placed in the CTM apparatus and recordings were secured.

The CTM apparatus, a modification of those used by Zweifel (1957) and Hutchison (1961), consisted of a variable transformer, a hemispherical heating mantle, a 3000 ml, three-necked distillation flask, and a centigrade thermometer calibrated to 1.0°. The flask was filled approximately half-full of aquarium gravel. The flask was then placed in the heating mantle and the variable transformer was adjusted so that the rate of heat-rise was approximately 0.5° per minute, i.e., slow enough to prevent heat shock, yet fast enough to prevent acclimation. Specimens were placed in the flask through the center neck, whereas the remaining two necks contained the thermometer and a short glass tube for the escape of expanding air. Body writhing or loss of righting response was taken as the point of CTM.

Population Size, Home Range, Migration, and Homing. In order to measure these interrelated parameters, five stations were chosen on Otter Creek. All specimens released at these stations were marked by a modification of the method used by Blanchard and Finster (1933), i.e., notching the scutes anterior to the vent with one, two or three notches. The resulting pattern was: A1, B1 . . . Zn, and combinations of the marks (A1–B1, D2–R3, etc.). The notches were incised with a small pocket clip designed for marking laboratory animals such as rats and mice.

Population densities at the stations were determined by the standard capture-release-recapture method devised and used by such workers as Petersen, Lincoln, and Jackson (Kendeigh, 1961).

The investigation of home range and migration resolved itself to keeping adequate records on the points of release and recapture of the marked individuals, and measuring the distance between these two points. The direction from the point of release to the point of recapture was also recorded (up, down, or across the stream).

Study Area Characteristics

The specimens used in this study were secured from three of the seven creeks that drain Madison County, Kentucky: Silver, Tates, and Otter.

Silver Creek, a tributary of Kentucky River, is formed southeast of Berea by the union of two forks. It flows 39.02 miles, has 60 tributaries, and drains approximately 83,000 acres. The banks are lined with a mixture of sycamore, tulip poplar, elm, beech, oak, box elder, maple, hickory, white ash and willow.

Tates Creek heads within Richmond city limits, and becomes confluent with the Kentucky River at Valley View, Kentucky. It flows 11.8 miles, repeatedly crossing State Highway 169 which parallels the stream for its entire course. The vegetation along its banks is similar to that of Silver Creek.

Otter Creek drains the northeastern portion of Madison County, its origin also lying within Richmond city limits; it flows into Kentucky River about two miles upstream from Fort Boonesborough State Park. The creek is formed by the convergence of three tributaries: Otter Creek proper, West Fork and East Fork. West Fork, heading near White Hall, merges with Otter Creek near Red House at the State Highway 388 crossing. East Fork, rising at Meadowview, merges with the main stream 1.5 miles farther downstream. The vegetation along Otter Creek is similar to that of Silver Creek.

Description of Stations

In the following discussion, the term "station" is used to designate collecting areas, although such areas often extend several hundred yards rather than being merely a sampling point. The food-preference study was conducted at two or more stations in all

TABLE 1. Capture sites for all specimens of *Regina septemvittata* discussed in text.

	STATIONS											
	Otter Creek					Tates Creek		Silver Creek				Totals Per
Month	1	2	3	4	5	1	2	1	2	3	4	Month
10/68	1	5	–	–	–	–	–	3	–	–	–	9
11/68	–	2	–	–	–	–	–	–	–	–	–	2
04/69	–	4	–	–	–	–	–	3	–	–	–	7
05/69	3	12	–	–	–	–	–	2	–	–	–	17
06/69	–	6	–	–	–	6	–	4	18	11	5	50
07/69	10	8	–	–	–	1	34	–	12	1	–	66
08/69	2	12	–	–	–	40	15	–	–	–	–	69
09/69	–	5	4	–	–	–	–	–	–	–	–	9
Totals Per Station	16	54	4	0	0	47	49	12	30	12	5	Grand Total 229

three creeks. Since the streams are very similar, only the location and most prominent characteristics of each station are noted. Due to the length of the stations, parameters such as stream width, depth and velocity, and rock size have little meaning and are omitted.

Silver Creek. Station I: at the first bridge on Barnes Mill Road, 6.7 miles west of Richmond; 500 yards. Station II: Taylor's Fork, 3 miles southwest of Richmond; 880 yards long. Station III: at point where Bogie Branch enters the creek, Barnes Mill Road, 8.5 miles northwest of Richmond; 400 yards long. Station IV: at end of Barnes Mill Road, 9.2 miles northeast of Richmond; 145 yards long.

Tates Creek. Station I: at Million, Kentucky on State Highway 169, 5.8 miles northwest of Richmond; 400 yards long. Station II: 0.5 mile downstream from Station I; 700 yards long.

Otter Creek. Station I: State Highway 388 crossing, Boonesboro, Kentucky, 3.1 miles above Boonesborough State Park; 210 yards long. Station II: 0.9 mile above Station I; 259 yards long. Station III: 0.4 mile above Station II (mouth of Stony Run Branch); 590 yards long. Station IV: East Fork of Otter Creek at State Highway 388 crossing; 335 yards long. Station V: main Otter Creek, 0.3 mile above Station IV (mouth of Lost Fork Creek); 150 yards long.

RESULTS

The snakes studied were hand-captured by overturning rocks during visits to the stations listed above. No schedule of station visitation was adhered to, although visits were made in all seasons, at various times and under various conditions. Several night visits were made (10 p.m. to 3 a.m.). By inspecting various other localities in Madison County, including farm ponds, still-water pools, and running water, the queen snake was found to frequent only permanent bodies of flowing water, a habitat type which seems to vary little throughout the snake's range (Raney and Roecker, 1947; Green, 1937; McCauley and East, 1940). The species has, however, been collected from non-flowing waters in Ohio (Conant, 1938a), Missouri (Anderson, 1965) and Illinois (Weed, 1922). Of the eleven collecting stations established by us, only two failed to yield specimens. No specimens were found in Otter Creek IV or V. These two stations were considerably dissimilar to the others; station IV provided abundant cover but was discontinuous and non-flowing during much of the summer, becoming almost completely dry during parts of July and August; station V was constantly flowing, but lacked sufficient cover for the snakes.

Table 1 lists all collecting stations and the number of specimens collected at each. Otter Creek II was collected most frequently and it yielded more specimens than any other station. Tates Creek II produced the most specimens per visit (average 16.3), whereas Silver Creek II was second (15.0) and Tates Creek I third (10.2). However, Silver Creek II included more than twice the area of Tates Creek I. The combined yield of these three stations was 126 snakes, or 50.6% of the total

specimens secured during the investigation. These stations are similar in make-up, all possessing shallow, slow-moving riffles with many small to large rocks. Tates Creek I lacks canopy cover, and Tates Creek II and the lower half of Silver Creek II are bordered by trees on one side only; their canopy cover varies between 10 to 20%. There is a complete absence of large deep pools and of steep, rapid waters, and the current is continuous throughout the year.

The queen snake, which Smith (1961) termed the stream counterpart of *Regina grahami*, is shy and difficult to capture except when encountered beneath rocks; the snake is an excellent swimmer. Our specimens were never located more than ten feet from water, and even then they were nearly always under rocks. There is some indication that temperature influences the distance at which queen snakes may wander away from water, i.e., the lower the ambient temperature the greater the distance from water. Our evidence on this point, however, is not conclusive and should be verified.

Of the 229 specimens taken during the study period, 95.6% were found beneath rocks, and in water versus on land in a 1.26:1 ratio. Only 1.8% of the specimens were found basking on rocks or on overhanging branches. Four specimens were excavated from a clay bank, four to 10 inches below the surface, in what appeared to be a network of crayfish burrows. Five snakes were encountered beneath other debris, and a large female was removed from a small hole in a sycamore tree, three feet above the waterline. From our field observations, Kentucky queen snakes appear to prefer a canopy cover of 0 to 50% (mean = 15%). Areas possessing cover greater than 50% seem to be avoided.

According to Raney and Roecker (1947) and Wood (1949), queen snakes are frequently found under rocks in gregarious gatherings of three or four specimens, often in the company of one or more *Natrix sipedon*. Wood (1944) described a prehibernation aggregation of 32 queen snakes in central Ohio, and Wood and Duellman (1950) reported similar aggregations from the same state in September, 1946. They collected 125 specimens from a shallow, rocky creek in a linear distance of 100 yards, locating as many as 24 specimens from a single site. Neill (1948) observed such an aggregation at Richmond County, Georgia. He suggested that the entire population of the creek was represented in this single aggregation. However, hibernation has apparently not been reported in the queen snake, although Conant (1938a) found a specimen lying on the January ice of a small creek in Ohio. Upon being warmed to room temperature, the snake appeared to be in good condition and continued living in captivity for several months thereafter.

On several occasions we found queen snakes under rocks with one or more *N. sipedon*. More often, however, we found assemblages of *N. sipedon* separated by short distances from similar groups of *R. septemvittata*. Moreover, *N. sipedon* seemed to be more abundant in rapidly flowing waters, whereas *R. septemvittata* was more or less restricted to quieter waters. Night observations indicated that although *N. sipedon* was active at that time *R. septemvittata* was nocturnally retiring. The specimens of the latter species were located under rocks.

Hibernation and Seasonal Activity. The literature, as touched upon above, contains very few reports on the seasonal activity of queen snakes. Conant (1938b) reported the first spring appearance as May 6, and the fall disappearance sometime in October. Raney and Roecker (1947) listed May 10 and September 23, respectively, as spring appearance and fall disappearance dates. In Kentucky, we found these dates to be April 5 and November 15 during the investigative period. The prehibernation aggregations mentioned above did not occur in our study areas, and we were unable to locate any hibernating snakes.

Food Preference. Following a one-week adjustment period, two tadpoles (*Rana* sp.) were placed in each experimental tank. One week later, six hard-shelled crayfish were added, three *Orconectes juvenilis* Hagen and three *Cambarus* sp. After three additional days had passed, three soft-shelled *Orconectes* were offered; no soft *Cambarus* were secured. Finally, a week later, six large meal worms (*Tenebrio* sp.) were placed in each tank. After two days, one of the tadpoles was eaten, but it was disgorged the same day with little signs of digestion. The only other food that was taken was two soft-shelled *Orconectes*. Three of the crayfish died and were left in

Table 2. Gut Analyses of 120 *Regina septemvittata* with Data Listed by Date and Collecting Station.

Date	Number Stomachs Examined	Number With Food	Percent With Food	Crayfish					*Etheostoma flabellare*	Percent of Total Food
				Cambarus	*Orconectes*	Not Determined	Total	Percent of Total Food		
6/69	40	38	95	4	20	25	49	96	2	4
7/69	40	38	95	1	24	19	44	100	0	0
8/69	40	34	85	0	25	28	53	100	0	0
Grand Totals	120	110	91.7	5	69	72	146	98.6	2	1.4
Tates Creek I	20	18	90	1	18	14	33	100	0	0
Tates Creek II	41	40	97.6	1	25	24	50	100	0	0
Silver Creek I	3	3	100	0	0	1	1	33.3	2	66.7
Silver Creek II	31	27	87.1	3	14	18	35	100	0	0
Silver Creek III	11	11	100	0	8	3	11	100	0	0
Otter Creek I	2	1	50	0	1	2	3	100	0	0
Otter Creek II	12	10	83.3	0	3	10	13	100	0	0
Stations										

the tanks, but the snakes made no attempt to ingest them.

Table II presents the results of gut analyses performed during June, July and August, 1969. Of the 120 stomachs examined, 110 (91.7%) contained food, 98.6% of which was composed of crayfish; the remaining 1.4% was comprised by two *Etheostoma flabellare* Rafinesque. Of the 146 total crayfish found, 72 (49.3%) were digested beyond recognition. The remaining 74 crayfish were diagnosed as *Orconectes juvenilis* (69, or 93.2%) and *Cambarus* sp. (5, or 6.8%).

Several guts contained the remains of more than one crayfish, but these were in the minority. Of the 108 guts containing crayfish, 81 (75%) had one each; 20 (18.5%) had two each; five (4.7%) had three each; one (0.9%) had four; and one large female from Tates Creek II contained six *O. juvenilis*.

By collecting at various times of the day, the investigators determined that feeding was most prevalent during the early morning hours (8 to 10 a.m.) and during the late afternoon (4 to 6 p.m.).

Gut analyses by station (Table II) demonstrated little variation in food habits. Three of the five *Cambarus* were removed from Silver Creek II specimens, and both fantail darters were taken from Silver Creek I snakes. There was no discernible difference in the types or amounts of food taken by the queen snake during the sampling periods.

Although these findings confirm the concensus of several investigators that the bulk of the queen snake's diet is crayfish, our examination of stomachs demonstrated little correlation between the size of the snake and the size of the prey taken, since small snakes often had very large crayfish in their guts.

During our food preference observations, a female queen snake approached a hard-shelled *Orconectes* and was immediately attacked and driven away, lending credence to the supposition that this snake probably could not catch and eat a well-armed, fully mature crayfish as suggested by Wood (1949). This may indicate either that the queen snake eats dead specimens or newly molted ones. A crayfish about to undergo ecdysis retreats to the cover afforded by rocks and at that time could be easily ingested by even a small queen snake. Some

evidence for this was furnished when we surprised a large snake beneath a rock in the water; the snake had partially swallowed a 2.5-inch soft-shelled *Orconectes*, which was abruptly disgorged. Other evidence comes from the food preference study, where we observed that only newly molted crayfish were eaten. We cannot support Wood's (1949) idea that queen snakes eat dead crayfish. Hall (1969) reported that *R. grahami* swallowed crayfish head-first and tail-first in a 1:1 ratio. Of all the crayfish taken by queen snakes during our study, only one had been swallowed head-first. This indicates that prey is taken from ambush rather than being caught by chase, or, that the crayfish were turned before being swallowed.

Contrary to the findings of Wood (1949), Raney and Roecker (1947). Conant (1960), and Burghardt (1968), all of whom indicate that crayfish of the genus *Cambarus* constitute most of the snake's diet, the queen snakes of Madison County, Kentucky feed almost exclusively on *Orconectes juvenilis*. These findings more or less parallel those of Penn (1950) who stated that 94% of New York, Pennsylvania and Virginia queen snakes contained *Orconectes obscurus* Hagen. In Kentucky, the reason for this is that the ratio of the two genera of crayfish in our study streams strongly favors *Orconectes*. Three of the five *Cambarus* found in the guts of snakes were from individuals collected at Silver Creek II. This station originates in Wilgreen Lake, the mud banks of which support a larger population of *Cambarus* than the environments at any of the other stations. Crayfish sampling demonstrated a ratio of 8.6:1 *Orconectes* to *Cambarus* at Silver Creek II, whereas at all other stations the ratio was about 9:1. Furthermore, most specimens of *Cambarus* were found either under rocks well away from the water or in burrows above the water line. This evidence indicates that the queen snake is an opportunistic feeder which takes any crayfish that presents itself. The inclusion of small vertebrates in the diet, such as tadpoles, is probably fortuitous rather than the result of active seeking.

Reproduction. Of 229 specimens examined, 113 were males and 116 were females, or essentially a 1:1 sex ratio. The sex ratio of young born in captivity (128) was 65 males and 63 females, also close to a 1:1 ratio. Fifty-seven of the females dissected for gut analyses were utilized to determine sexual maturity. Thirty-five contained immature eggs, mature eggs, or embryos, or had recently given birth to young (Fig. 1). The number of young that had been presented by each female was ascertained by counting the stretched pockets in the oviducts. The 35 specimens contained from 7 to 49 (mean = 25.1) immature eggs. Fifteen specimens (42.8%) contained only immature eggs; most of these specimens were captured during June and July. However, one snake, containing seven eggs, was captured on August 13. Only two specimens (5.7%) contained immature and mature eggs, and both were captured during June. Four snakes (11.5%), three of which were taken in August and the other one in June, contained immature eggs and embryos. The last 14 specimens (40%), all taken August 12–13, contained immature eggs and had given birth. The number of young per litter varied between 7 and 17, totaled 163, and averaged 11.6 per litter.

Another criterion which has been utilized for the determination of sexual maturity is size. Wood and Duellman (1950) considered 375 mm total length as the point between maturity and immaturity. Generally, this was true of our specimens, as confirmed by dissection, but one 344 mm female contained 10 immature eggs. This is probably, however, near the minimal size for a sexually mature queen snake. The largest snake which lacked eggs was 454 mm total length, captured on August 12, 1969. The total length of 18 immature specimens ranged from 242 mm in June to 454 mm in August (mean = 315). These specimens were doubtless in their first year of growth. The 344 mm specimen falls into this category, thereby presenting some evidence that young females may develop a few immature eggs late in the fall of their first year. Specimens containing only immature eggs ranged from 344 mm to 592 mm (mean = 507.4) in total length and, with the possible exception of the 344 mm and 376 mm specimens, evidently were in their second year of growth. Specimens containing mature eggs, embryos, or ones which had given birth to young, ranged from 585 mm to 757 mm in total length (mean = 677.2), and we judged them to be in their third or subsequent year. How-

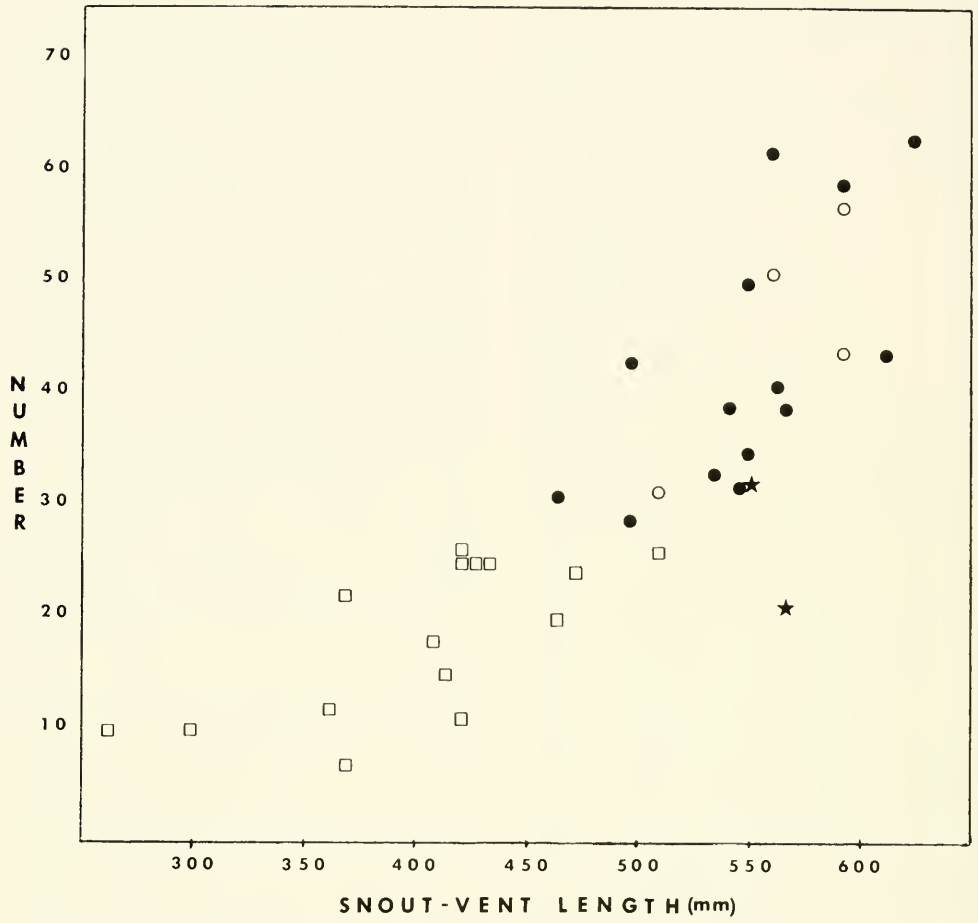

Figure 1. Snout-vent lengths of 35 *Regina septemvittata* correlated with numbers of mature and immature ovarian eggs, embryos or young. Squares = specimens with immature eggs only; stars = specimens with both immature and mature eggs; open circles = specimens with immature eggs and embryos; closed circles = specimens with immature eggs which had presented young.

ever, age cannot be accurately determined by size beyond the third year due to reduction in growth rate (Wood and Duellman, 1950).

Our evidence indicates that female queen snakes generally do not reach sexual maturity until the second year of life, and that they probably do not reproduce until the third year. Mating probably occurs during the fall of the second year or in the spring of the third. As far as we were able to determine from development of the testes and seminal vesicles, and from growth patterns, male queen snakes also become mature during their second year and probably mate that fall, or during the spring of their third year. However, sperm smears were not made to substantiate this deduction.

The presence of immature eggs in specimens which had produced litters possibly indicates that such eggs represent the following year's litters, and further, that immature eggs are produced at least one year in advance of reproduction. If true, the validity of our hypothesis regarding the age at onset of reproduction in female queen snakes should be obvious. Tinkle (1962) observed this type of cycle in *Crotalus atrox* Baird and Girard in Texas, indicating that the female usually does not have energy reserve to produce broods each year. However, in light of

Table 3. Place of Capture, Weight, and Total and Snout-Vent Lengths of Mothers of Ten Litters of Young, and Birth Dates and Number of Young. Lengths in mm; Weights in gms.

Young			Mothers			
				Length		
Litter	Number	Birth Date	Place of Capture	Total	Snout-Vent	Weight
1	16	8/04/69	Otter Creek I	725	585	83.0
2	14	8/04/69	Otter Creek I	699	585	71.5
3	11	8/04/69	Otter Creek I	643	502	59.8
4	11	8/05/69	Otter Creek I	776	636	122.1
5	13	8/11/69	Otter Creek II	840	678	137.8
6	13	8/13/69	Otter Creek II	738	662	116.2
7	17	8/18/69	Otter Creek II	785	645	113.5
8	12	8/20/69	Tates Creek II	711	571	89.8
9	13	8/20/69	Tates Creek II	674	560	84.4
10	8	9/10/69	Otter Creek II	630	501	56.2

our information this is probably not true for the queen snake which we believe produces annual litters following the onset of maturity.

Dissection of several gravid females revealed that viviparity in the queen snake involves more than mere retention of eggs. At all stages of development, the eggs lacked a shell. In specimens with oviducal eggs, the thin chorionic membrane was in intimate contact with the distended oviduct and both became richly supplied with a fine network of blood vessels. Comparison of oviducal eggs at different stages of development demonstrated a notable increase in size, which suggested placental transmission of dissolved solids, an observation similar to that of Hall (1969) in *Regina grahami*, and Clark et al. (1955) in *Thamnophis sirtalis* (Linnaeus).

When the total number of eggs, embryos, and young from each adult are plotted against individual snout-vent lengths (Fig. 1), it can be seen that the number increases with increasing body length. The smallest specimen (344 mm) containing eggs (10) was captured July 7 at Tates Creek II, whereas the largest snake, a 764 mm specimen, was collected on August 12 at Tates Creek I; it contained 49 immature eggs, had given birth to 14 young, and thus presented a combined total of 63. Figure 2 also demonstrates that 75% of the snakes containing mature eggs or young had body lengths of 500 to 600 mm.

Ten gravid females captured during July and August presented young in captivity (Table 3). The number of young per litter varied from 8 to 17 (mean = 12.8), and delivery dates ranged from August 4 to Sep-

Table 4. Statistical Analysis of Length and Weight, by Litters and Sex, of Newborn *Regina septemvittata*. Lengths in mm; Weights in gms; S = standard deviation; $S_{\bar{x}}$ = standard error of mean; $\bar{x}$ = mean.

		Snout-Vent Length				Weight			
Litter	Number	Range	$\bar{x}$	S	$S_{\bar{x}}$	Range	$\bar{x}$	S	$S_{\bar{x}}$
1	16	134–169	159	8.24	2.06	2.400–2.911	2.794	0.137	0.034
2	14	157–170	165	4.31	1.15	2.517–3.065	2.835	0.131	0.035
3	11	157–170	164	3.95	1.19	2.630–2.910	2.804	0.094	0.027
4	11	160–171	165	3.45	1.04	2.664–2.953	2.808	0.086	0.026
5	13	192–204	198	4.63	1.28	3.356–4.216	3.791	0.345	0.096
6	13	180–192	187	3.90	1.08	3.162–3.800	3.609	0.152	0.042
7	17	177–203	186	6.25	1.52	3.110–4.015	3.614	0.267	0.065
8	12	170–210	184	9.86	2.84	3.150–4.071	3.600	0.254	0.073
9	13	162–200	178	12.40	3.44	2.465–3.912	3.254	0.495	0.137
10	8	180–202	191	7.83	2.77	3.476–4.003	3.744	0.189	0.067
Males	65	134–210	177	15.69	1.94	2.400–4.199	3.255	0.487	0.060
Females	63	159–203	178	13.55	1.70	2.630–4.216	3.296	0.059	0.007
Combined	128	134–210	177	14.59	1.29	2.400–4.216	3.279	0.477	0.042

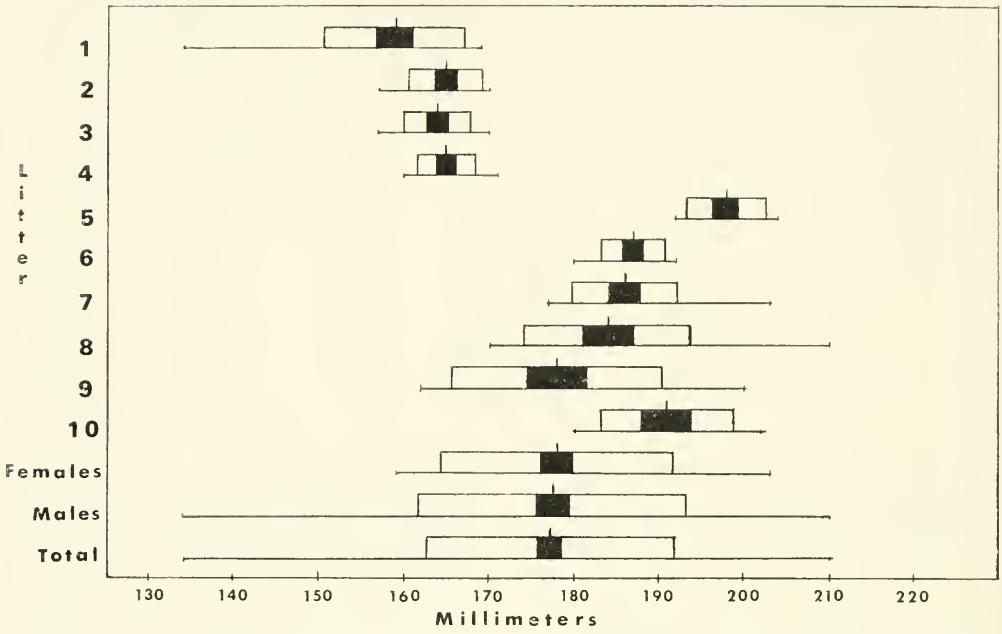

Figure 2. Snout-vent length data for young *Regina septemvittata* (see Table 4). Horizontal line = range; vertical line = mean; open box = standard deviation mean; filled box = two standard errors on each side of mean.

tember 10. Dunn (1915) reported 5 per litter in Virginia, Triplehorn (1949) 23 per litter in Ohio, and Funkhouser (1925) stated that broods of 30 to 40 were not uncommon in Kentucky snakes. Additional reported measurements for newborn queen snakes may be found in Hudson (1954), Anderson (1965), Wood (1949), Swanson (1952), McCauley (1945), Conant (1938b), and Minton (1944). Several reports of number of young have been published, including those of Pope (1944), and Barbour (1968) who gave a range of 5–18. Total and snout-vent lengths for our observed litters are compared in Table 4 and in Figs. 2 and 3. Although sex ratios varied widely within a given litter, the total number (128) numbered 63 females and 65 males, or very close to a 1:1 ratio. As shown in Table 4, the weight varied between 2.400 gms and 4.216 gms (mean = 3.279).

The only records for newborn queen snakes are those of Burghardt (1968). A litter of 20 young, born August 18 in Illinois, averaged 161 mm in snout-vent length and 2.937 gm in weight. Our data for snout-vent length is presented in Figure 2, and that for weight in Figure 3. Litters one through four differ from litters five through 10. The mothers of the first four litters were collected at Station I of Otter Creek (Table 3). Litter one, presented a few days prematurely differs slightly from litters two, three and four (Figs. 2, 3). Litters five and 10 differ from litters six, seven, eight and nine, both in length and weight. Table 3 also demonstrates that the mother of litter five was much larger than the other females, and that litter 10 was produced on September 10, at least three weeks later than the others. Although the 10 litters differed considerably among themselves, there was no obvious difference between males and females, and neither sex differed in these particulars from those of the combined total.

The process of birth was observed in eight of the 10 litters born in captivity. As the female became ready to present young, pronounced swellings developed at the posterior two-thirds of the body. Gentle convulsive twitchings affected the same area. During presentation of young, the vent was raised two to three cm and the tail was arched and moved slowly from side to side as the con-

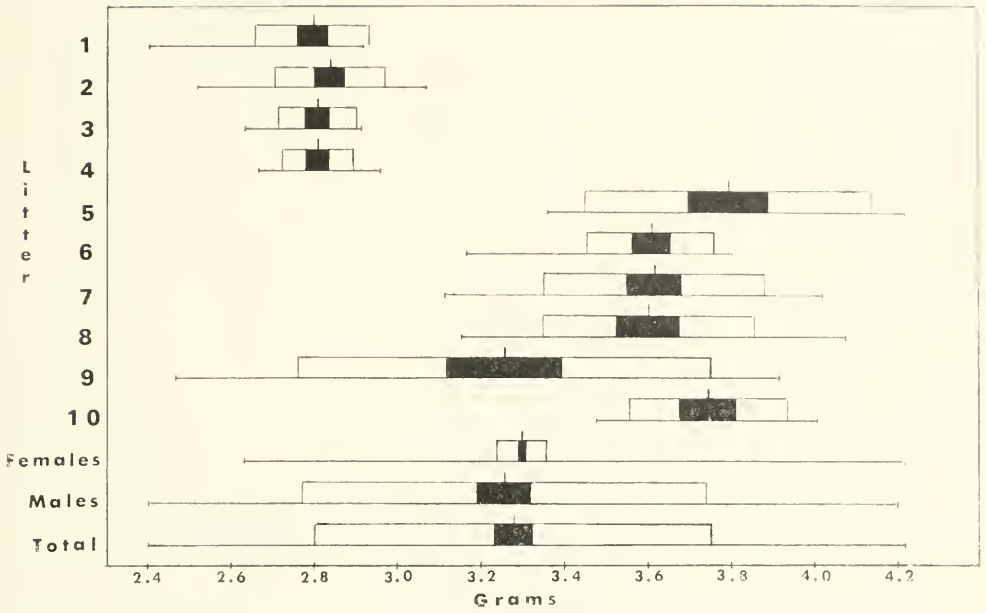

Figure 3. Body weight data for young *Regina septemvittata* (see Table 4). Symbols as in Fig. 3.

vulsive waves passed caudad. The amnion sac appeared first, followed by the allantois and the yolk sac. In many cases the young snakes broke the amnion sac before being completely delivered, depending upon delivery position. Some young were presented head-first and some body-loop first. Those that did not break the sac by forcing their heads through it during birth did so within seconds after delivery.

The females did not always remain in the same place while presenting young, sometimes crawling around the cage, stopping periodically to present another young. The mother snakes did not pay much heed to their young, and crawled over them repeatedly. However, this may be a reflection of captivity.

The time required for individual births ranged from 1.5 minutes to 2.5 minutes, and the time-lapse between births ranged from four minutes to one hour (mean = 11 minutes). There seems to be no special time of the day during which young are presented. Of the 10 litters, four were presented between 6:00 a.m. and noon, four between noon and 6:00 p.m., and two litters were presented during the night.

Within seconds after breaking the amnion with the head, each young snake opened its mouth widely, and breathing rhythms and tongue flicks followed immediately. No attempt was made to determine breathing or heart rates in the young. The umbilical cord was attached to the yolk sac and to the young snake at a point about 15 mm anterior to the vent. The young snakes were capable of frolicking and swimming moments after birth, and the amount of activity determined how long the umbilical cord remained attached. In some cases, the yolk sac was dragged about for three to four hours. Within 24 hours after birth, all young completed shedding the thin skin. Another molt involving a thicker skin followed approximately four days later.

All 16 snakes of the first litter were prematurely born, and were unable to break the amnion. Considerably more yolk remained in the yolk sac of these specimens than in those of the other litters. Two of these premature snakes, still contained in the amnionic sac, were alive after 10 hours. Efforts to free them succeeded, but they soon died. One male had a fused body loop and a total body length of 172 mm.

A method for sexing the young was devised in which the snake was turned ventral

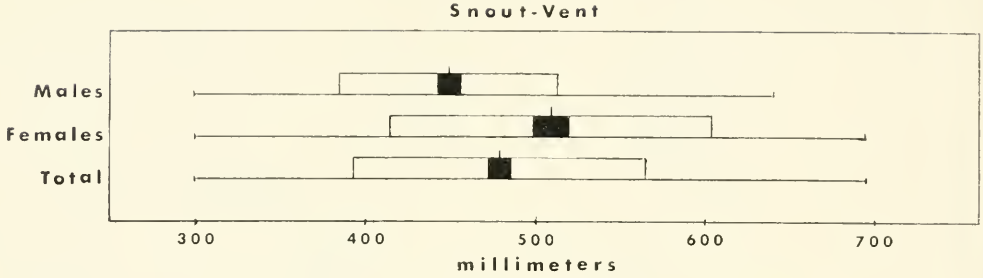

Figure 4. Snout-vent length data for adult *Regina septemvittata*. Symbols as in Fig. 3.

side up and the right thumb placed slightly posterior to the vent with the forefinger resting beneath the specimen's back. A moderate pressure applied by this method caused the hemipenes of the males to become everted.

Although the young queen snakes refused to feed in captivity, our field investigation revealed that young-of-the-year in the wild do feed between the time of birth and hibernation, and in every case the food was soft-shelled *Orconectes*.

Size and Growth Rate. Comparing snout-vent lengths for our data on 179 adult snakes (90 males; 89 females) showed that the sexes differed (Fig. 4), ranging from 299 to 642 mm (mean = 448.9) in males, and from 299 to 695 mm (mean = 509.1) in females. Smith's (1961) measurements of 30 Illinois snakes indicated that the tail occupied 26 to 28.6% (mean = 27.2) of the total length in 10 males and 19.9 to 26.9% (mean = 24.5) in 20 females, and Wood and Duellman (loc. cit.) reported 23.0 to 29.0% (mean = 25.0) for 73 Ohio males and 19.6 to 26.5% (mean = 22.8) for 60 females.

The literature is meager on queen snake growth rates. One estimate (Raney and Roecker, 1947) was based upon 17 recently born specimens, 217 mm in average length, and 21 yearlings averaging 390 mm in length; the calculated average increase in length was 173 mm, or 79%. Raney and Roecker thus indicated that the growth rate in the queen snake was about the same as in *Natrix sipedon*. Blanchard and Finster (1933), however, found that the annual increase in Michigan populations of *N. sipedon* was about 50% in the young, but only approximately 15% in adults; by the third year, the increase was less than 33%. These findings were substantiated in Ohio queen snakes by Wood and Duellman (1950), who reported an increment of 50% during the second year and diminishing growth rates during the third and subsequent years. All writers seem to agree that female queen snakes have a greater annual length increment than males, and they may also attain a greater maximum length.

Maximum size has been listed for *Regina septemvittata* in various parts of its range (Conant, 1938a; McCauley, 1945; Pope, 1944; Triplehorn, 1949; and Wood and Duellman, 1950). The record length appears to be a 922 mm (36.25 inches) female from near Defiance, Ohio (Triplehorn, 1949). The minimum size for a sexually mature queen snake has not been determined, although Wood and Duellman (1950) consider 375 mm as the cutoff point between juveniles and adults.

When the mean total length of our newborn snakes is compared to that of yearlings (242 to 454 mm; mean = 398), an average growth increment of 171 mm, or 75%, is calculated. These data closely approximate the 79% reported by Raney and Roecker (1947) for New York specimens. The mean total length for specimens judged to be in their second year was 576 mm. Comparing this calculation with the mean total length of the yearlings, a putative growth increase of 178 mm, or 44.8%, was computed. This is slightly less than the 50% calculated for Ohio specimens by Wood and Duellman (1950).

Length measurements did not clearly differentiate a third-year class and, therefore, growth for this age group could not be calculated. Growth rates in adult *R. septemvittata* were determined by our capture-release-recapture investigation. A 615 mm specimen released October 24, 1968 and recaptured on July 16, 1969 measured 712 mm

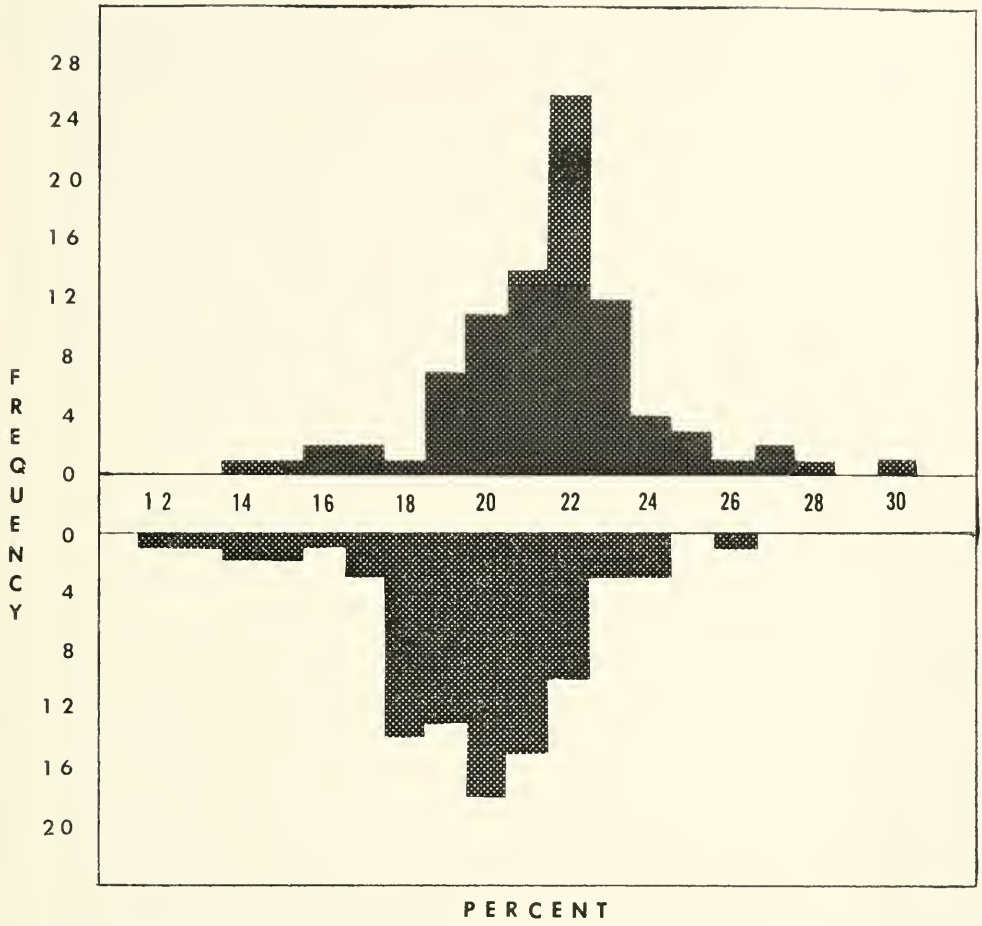

Figure 5. Histograms of tail length/total length for 90 male and 89 female adult *Regina septemvittata.*

in total length, or an increase of 97 mm (15%) over a period of 38 weeks. Similarly, a 738 mm female increased to 840 mm during 42 weeks of freedom (102 mm), or 14%. These figures are close to those of Blanchard and Finster (1933) for adult *Natrix sipedon* (15%), but greater than the 5% reported for *Thamnophis sirtalis.* However, an 850 mm female grew only 5 mm during a period of 42 weeks, or an increase of 0.6%. These data support the idea that older individuals grow more slowly than younger ones. The first specimen recaptured was probably in its fourth season, the second in its fifth, and the third in its sixth or some subsequent year. Other recaptures involved shorter periods of time during summer months only, thus could not be used to determine annual growth rates. It is interesting, however, that the summer growth rates for such individuals averaged approximately 2.5 mm per week.

Body Temperature and Critical Thermal Maxima. There seems to be no literature reports on queen snake body temperatures. The specimens were found both in and out of water, therefore, the ambient temperature (Fig. 6) reflects both habitats. Of the 205 specimens, 116 (56.6%) were partially or completely submerged in water, whereas 89 (43.4%) were found out of water. All specimens found in water expressed temperatures ranging from 0.2 to 6.2 degrees (mean = 2.4) above water temperatures. Of the 89 specimens found out of water, 60 (67.4%) had temperatures lower than ambient ones (14.2% of the total number). The highest

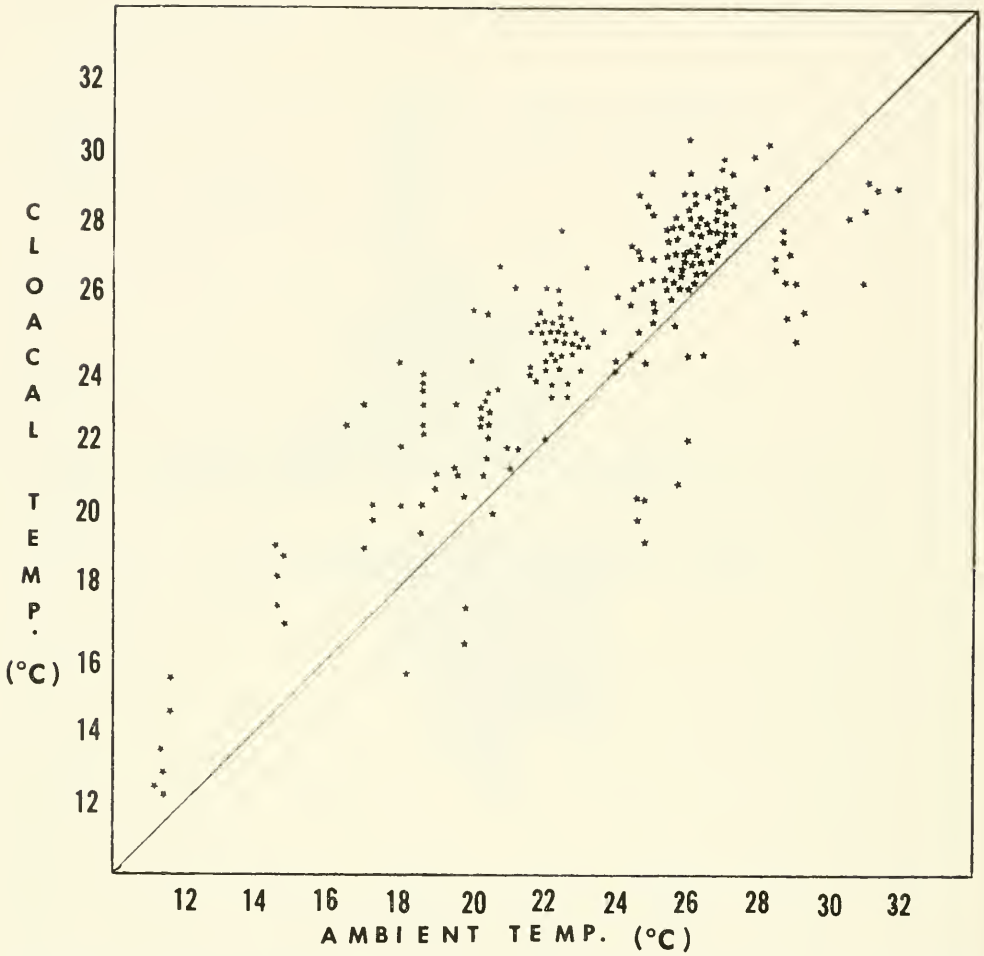

Figure 6. Cloacal temperatures of 205 *Regina septemvittata* compared with ambient temperatures. Diagonal line represents point at which cloacal and ambient temperatures are equal. Stars above line represent specimens with cloacal temperatures higher than ambient; stars below line are specimens with cloacal temperatures lower than ambient.

body temperature recorded during the study was taken on June 30, 1969 from a specimen found in water of 26° C (air 30.8°), 30.4° C. The lowest body temperature was 12.2° C, recorded October 24, 1969 when the air temperature was 8° C and that of the water 11.2°. The mean temperature of all recordings was 25.6° C.

The 29 measurements appearing below the equatorial line in Figure 6 were taken from specimens found under rocks away from water, and the ambient temperature was recorded in the air approximately four feet above ground level. Had these temperatures been measured in the cooler areas beneath the rocks, these 29 specimens perhaps would have also demonstrated body temperatures higher than the ambient. From these observations, it seems evident that *R. septemvittata* can exert some control over its body temperature, maintaining temperatures of at least 6.2° C above the ambient. Lueth (1941) felt that most snakes were able to maintain body temperatures above ambient ones of 0° to 10° C and below ambient temperatures of 30° C. Our data also indicate a correlation between body size and body temperatures, smaller individuals generally showing higher

TABLE 5. Critical Thermal Maxima Comparisons Between 10 Adult and 10 Juvenile *Regina septemvittata*. Temperatures in Centrigrade; Times in Minutes; Weights in gms; Lengths in mm: A = Adult; J = Juvenile.

Specimen Number		1	2	3	4	5	6	7	8	9	10	Mean
Initial Flask	A	25.0	25.0	25.0	25.0	25.0	25.0	25.0	25.0	25.0	25.0	25.0
Temperature	J	25.5	25.5	25.5	25.5	25.0	25.0	25.0	25.0	25.0	25.0	25.0
Temperature	A	44.0	43.5	43.5	44.5	44.0	44.0	44.5	43.5	44.0	43.5	43.9
at CTM	J	39.5	40.5	40.0	41.5	40.5	39.5	40.5	40.5	40.0	41.0	40.3
Time to CTM	A	25.0	24.0	21.5	25.0	26.0	25.5	26.0	25.0	25.5	25.0	24.9
	J	19.0	19.5	19.0	20.0	19.5	19.0	19.5	19.0	19.0	19.5	19.3
Initial Cloacal	A	22.5	21.0	22.0	22.4	21.4	22.8	23.2	22.4	22.6	24.2	22.5
Temperature	J	26.4	25.0	26.8	25.2	25.3	27.2	25.8	25.5	26.6	27.0	26.0
Body Weight	A	55.7	118.8	44.8	89.2	59.1	59.6	88.4	43.2	98.1	25.5	68.2
	J	3.97	4.31	4.26	5.05	4.59	3.84	4.10	4.25	4.05	4.84	4.33
Snout-Vent	A	510	630	455	553	520	515	635	441	580	377	522
Length	J	152	187	184	201	188	148	188	168	160	205	178

temperatures than larger ones. This shall have to be substantiated by more intensive investigation.

Table 5 presents the results of a comparative ctm study between 10 adult and 10 juvenile queen snakes. Initial flask temperatures, time to CTM, and initial cloacal temperatures were taken and recorded to assure that each specimen was tested under similar conditions. For the adults, CTM ranged from 43.4 to 44.5° C (mean = 43.9), while that for juveniles ranged from 39.5 to 41.5° C (mean = 40.3). The data (Table 5) show little or no correlation between body weight or size and the temperature at which the adults reached CTM. However, in the juveniles, where weights and lengths exhibited a much smaller range, there were distinct correlations between body weight and CTM and length and CTM (Table 5). The CTM of juveniles appears to be directly proportional to body weight and length.

It is a well-established principle in reptiles (Lowe and Vance, 1955; Hutchison, Vinegar and Kosh, 1966) and amphibians (Zweifel, 1957; Hutchison, 1961; Brattstrom and Lawrence, 1962) that the temperature to which an animal has been acclimated exerts a significant effect on the level of temperature at which the animal reaches CTM. In this investigation, since the 20 specimens tested were captured at the same hour, at the same location and, in some instances, under the same rock, it was assumed that their thermal histories were the same and, therefore, did not affect the results of testing. Brattstrom and Lawrence (loc. cit.) and Hutchison, Vinegar and Kosh (loc. cit.) reported that CTM depends upon the size of the animal, and that smaller specimens demonstrate higher CTM's. This work, however, disputes these reports in that the larger juvenile queen snakes (determined by weight and length) exhibited higher CTM than the small ones (Fig. 1). Hutchison (1961) found no correlation between body size and CTM in adult salamanders. Our testing indicated no correlation between adult size and CTM, although it did demonstrate a higher heat tolerance in adults than in juveniles. Although a temperature above 43.9° C is required to cause death in adults, the highest voluntary body temperature recorded was 30.4° C. Little is known about the critical thermal minima of the queen snake, although Lueth (loc. cit.) reported these minima as −2° to −5° C in *Natrix sipedon*. The lowest voluntary body temperature recorded for the queen snake during our work was 12.2° C.

Population Size, Home Range, Migration, and Homing. Because of inadequate recapture, population size was established only at stations I and II of Otter Creek. The average population at Station I was 35, whereas at Station II it was 62. Table 6 records 13 recaptures involving 10 specimens. The queen snake seems to have a relatively small home range, but shows some tendency to dispersal. Of 13 recaptures, the straight-line distance from point of release to point of recapture varied from about 10 feet to 450 (mean = 74.2), although 11 of the 13 were less than 100 feet. Specimens one and 10 were recaptured twice. Specimen

Table 6. Movements and Growth Rates of Marked *Regina septemvittata*. Lengths in mm; Distances in Feet; Time in Weeks. Snakes 47, 51 and 65 were from Otter Creek I; the remainder were from Otter Creek II.

Specimen Number	Sex	Length When Released	Date of Release	Interval Before Recovery	Length When Recovered	Minimum Distance Traveled
1	F	615	10/24/68	27 wks.	662	50 ft.
1	F	662	05/02/69	11 wks.	712	150 ft.
3	M	555	10/24/68	1 wk.	557	35 ft.
4	F	850	10/24/68	42 wks.	855	75 ft.
10	F	738	11/01/68	37 wks.	795	50 ft.
10	F	795	07/16/69	5 wks.	840	25 ft.
43	M	668	06/24/69	7 wks.	674	35 ft.
46	M	649	06/24/69	7 wks.	674	40 ft.
47	F	643	07/15/69	1½ wks.	645	10 ft.
51	F	776	07/15/69	1½ wks.	789	20 ft.
54	F	789	07/16/69	3½ wks.	814	15 ft.
56	M	624	07/16/69	3½ wks.	649	10 ft.
63	M	617	07/24/69	2 wks.	635	450 ft.

one was initially released October 24, 1968, and was recaptured the following spring, May 2, 1969, on the same side of the stream but 50 feet farther upstream. The second recapture was made July 16, 1969, when the snake was found on the opposite side and 150 feet upstream from the point of the second site. The total minimum distance traveled from initial release was 200 feet upstream over a period of 38 weeks. Specimen two was initially captured and released about midway in Station II on November 1, 1968. This female was recaptured July 16, 1969 approximately 50 feet downstream from the point of release; the second recapture was made on August 7, 1969 on the opposite side of the stream, 25 feet upstream from the point of the first recapture. The total minimum distance traveled from the initial release point was 75 feet, but the net distance was slightly more than 25 feet over a period of 40 weeks.

We have no definite evidence of migration, since all recaptures were made in the same vicinity of initial release. However, during the investigation on homing, in which specimens were transported from station to station, no specimens were recaptured. Seven individuals, initially captured at Station II, were marked and released at Station I on May 1, 1969. The same day, six specimens were transported from Station II to Station IV. The following day, three specimens were removed from Station I to Station II. Likewise, specimens brought in from stations on Tates and Silver creeks were never recaptured. On May 14, 1969, two specimens captured at Silver Creek I were released at Otter Creek I, and on June 10, 1969, six specimens were transported from Silver Creek IV to Otter Creek IV. Also, seven specimens were taken from Tates Creek II to Otter Creek II on July 26, 1969, and on August 20, 1969 eight snakes were removed from Tates Creek I to Otter Creek III. A total of 49 specimens were, then, relocated in Otter Creek, but none of these were recaptured. This indicates that these snakes did disperse, but there was no evidence as regards direction, distances, etc.

Predation and Ectoparasites. It is very likely that queen snakes may be preyed upon by mice (Wood, 1949) and by other snakes (Huheey and Stupka, 1967) during hibernation. Young snakes are perhaps subject to considerable predation at any time. For example, several of the snakes born in captivity were killed and eaten by the crayfish which had been placed in the tanks as food for adults. Apparently, the crayfish caught and successfully held the young snakes beneath the water until they drowned. On several occasions crayfish were observed attempting to attack the adult snakes. Another instance of predation of young queen snakes was reported by Mr. Ronald Houp, a graduate student at Eastern Kentucky University, in which a hellbender, *Cryptobranchus alleganiensis* (Daudin), was found to have eaten two individuals.

Although all water snakes are subject to numerous parasites (Holl and Allison, 1935),

only two types were discovered during our study. Many specimens had numerous white blisters scattered over the body. These blisters increased in number as the snakes prepared to molt, following which most of the blisters were sloughed off with the skin. However, a few remained to reinfect the snake. Individuals kept in captivity developed greater numbers of this parasite than ones secured from nature. Incubation of the contents from one of these blisters proved the parasite to be an undiagnosed species of the fungus genus *Verticellium*. The second instance of parasitism involved a male snake captured in mud, which bore three leeches, probably *Placobdella rugosa* (Verrill), attached to the neck region.

Summary and Conclusions

The results of our investigations and measurements are reviewed and summarized as follows: *Regina septemvittata* is mildly dispositioned and seldom attempts to bite even during rough handling. The primary means of defense are secretive habits, escape by swimming rapidly and hiding under water, and the utilization of musk glands located on either side of the cloaca. The preferred habitat is constantly flowing streams possessing an abundance of cover, i.e., medium to large, flat rocks, and accompanied by a canopy cover that averages about 15%, seldom exceeding 50%. The snake is seldom found in riffles with a steep gradient, slow riffles and shallow pools being preferred. Although occasionally encountered sunning on rocks and overhanging tree branches, the highly aquatic queen snake was most often found beneath rocks, both in and out of the water, seldom more than 10 feet from the streams. It is not a particularly nocturnal animal.

Regina septemvittata is moderately gregarious, with aggregations of two to four specimens occasionally being observed beneath the same rock, sometimes accompanied by one or more *Natrix sipedon*.

The bulk of Kentucky queen snakes' diet (98.6%) is composed of soft-shelled crayfish, 93.2% of which is *Orconectes juvenilis*. Only on three occasions were other foods observed: two fantail darters and a ranid tadpole. The snake is probably an opportunistic feeder, preying upon the most abundant crayfish in the habitat. Prey are taken from ambush rather than by chase, or the crayfish are turned before swallowing, as determined by attitude in the gut. Feeding was more frequent between 8:00 a.m. and 10:00 a.m., and between 4:00 p.m. and 6:00 p.m. than at other times of the day. Food habits varied little between collecting stations and different times of the year. Young-of-the-year also utilized soft-shelled *Orconectes juvenilis*.

A 1:1 sex ratio, both in adults and in newborn was observed. Females generally do not reproduce until their third year, although immature eggs may be found early during the second year, and possibly are produced in late fall of the first year. The minimum size of a mature female observed was 344 mm total length. Males appear to become sexually mature during the second year. Mating probably occurs both in spring and fall, with young females mating for the first time during the fall of their second year or in the spring of their third year. Dissected females contained from 7 to 49 immature eggs, in addition to mature eggs or embryos, or were recognized as having given birth. The immature eggs probably represent the reproductive potential for the following season, thus indicating an annual reproductive cycle rather than a biannual one. The total combination of eggs, embryos, and empty follicles (young produced) increases proportionally with body size.

The queen snake is viviparous, and the retained eggs lack shells at all stages of development. The thin chorionic membrane of oviducal eggs lies in intimate contact with the distended oviduct during development. A notable increase in egg size indicates transmission of dissolved nutrients. The young were born in captivity from August 4 to September 10, 1969, the number per litter varying from 8 to 17, averaging 12.8 per female. During parturition, the amnion sac appears first, then is followed by the allantois and yolk sac. The young were presented either head- or body-loop first, and most of the young snakes broke the amnion sac during the process of birth or moments thereafter. The time required for parturition ranged from 1.5 to 2.5 minutes, with a lapse of four minutes to one hour between births. There was no indication of maternal concern for the newborn, which were capable of frolicking and swimming within seconds after birth. These movements effect elimi-

nation of the umbilicus cord a short time after birth. All newborn snakes shed their fetal (very thin) skin within 24 hours following birth, and a thicker skin is shed four days later. The sex of the young snakes was determined by pressure-eversion of the hemipenes. New-born weights varied from 2.400 to 4.216 gms (mean = 3.279), whereas total lengths ranged from 172 to 265 mm (mean = 227).

Growth rates were highest during the first year, with yearlings showing an average increase of 75% length increase over newborn. The percentage increase for the second year class averaged 44.8. No definite third year class was distinguishable, so annual growth estimates at that level were not possible. However, the total growth was about 14 to 15% for the older specimens, regardless of age. Summer growth rate, as determined by marking experiments, was approximately 2.5 mm per week. Female queen snakes grow faster than males and they attain larger sizes.

Cloacal temperatures in the queen snake were found to be higher by as much as 6.2° C than ambient temperatures, indicating a tendency to temperature regulation. The highest recorded body temperature was 30.4° C, and the lowest 12.2°. The mean cloacal temperature for all snakes was 25.6° C, which must be considered in light of prevailing ambient temperatures. The critical thermal maxima for adult queen snakes varied from 43.4° C to 44.5° (mean = 43.9), whereas that of juveniles ranged from 39.5° to 41.5° (mean = 40.3), indicating that larger snakes have a higher temperature tolerance than juveniles. Body size apparently does not affect the CTM of adults, but in juveniles it appears to be proportional to body weight and length.

Population size was calculated to be 35 per 210 yards at Otter Creek, and 62 per 259 yards at another point on the same creek. Home ranges are relatively small, although definite sizes were not determined. Homing tendencies were indicated in two examples, although translocated specimens were never recaptured.

Hibernacula were not observed. The first spring-appearance date in Kentucky queen snakes was April 5, and the fall-disappearance date was November 15. No prehibernation aggregations occurred.

Adult queen snakes are subject to predation by crayfish and mice during hibernation, and by other snakes during the active season. Juveniles were observed being preyed upon by crayfish, and young snakes were found in the gut of the hellbender, *Cryptobranchus alleganiensis*.

Two ectoparasites were found on the queen snake: a fungus of the genus *Verticellium*, and a leech, *Placobdella rugosa*.

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ETHEOSTOMA BOSCHUNGI, A NEW PERCID FISH FROM THE TENNESSEE RIVER DRAINAGE IN NORTHERN ALABAMA AND WESTERN TENNESSEE

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ABSTRACT

Etheostoma **boschungi**, the slackwater darter, is described from 110 specimens taken from second and third order streams in the southern bend of the Tennessee River. It appears to be an eastern representative of a species group whose other members, *E. punctulatum, E. cragini*, and *E. pallididorsum*, are found in western drainages of the Mississippi River Basin. *E. boschungi* differs from its western relatives in details of pigmentation, squamation, and osteology.

INTRODUCTION

In 1968, Dorothy A. Sentz of Florence, Alabama brought to our attention an undescribed species of darter which she and Charles Gooch had collected from Lindsey Creek, a tributary of Cypress Creek of the Tennessee River system in Lauderdale County, Alabama.

Subsequently, we visited Lindsey Creek and obtained additional specimens. Shortly thereafter, Charles Gooch informed us of specimens that he had taken during the summer of 1968, in the course of a survey he was conducting of the fish fauna of the Cypress Creek drainage.

Following presentation of our discovery at the meeting of the Southeastern Division of the American Society of Ichthyologists and Herpetologists in April of 1969, Ralph Yerger informed us that he had, on loan from the University of Tennessee, a collection of darters which included a single specimen that closely resembled the species we were describing. We examined the specimen, which had been collected by David Etnier and his students in August 1967, from the Buffalo River, and found it to be conspecific with the specimens from Lindsey Creek. In the Fall of 1969, David Etnier informed us that R. B. Fitz, of the Tennessee Valley Authority, had collected the species in the Flint River, Madison County, Alabama.

We acknowledge with gratitude the assistance of the persons noted above who advised us of collecting localities and supplied specimens for examination. We are indebted to a number of other persons who provided aid in various ways. Albert P. Blair loaned preserved specimens and color transparencies of *Etheostoma cragini*, Frank B. Cross loaned preserved specimens of *E. cragini* and *E. pallididorsum*, and color transparencies of *E. cragini* and *E. punctulatum*, Glenn H. Clemmer and W. Mike Howell provided specimens of the darter being described, assisted in the field, and reviewed the manuscript, Carter R. Gilbert loaned specimens of the darter being described, and Franklin F. Snelson loaned color transparencies of *E. cragini* and *E. punctulatum*. Gene Beckham, Hector Harima, and Maurice Mettee assisted in the field work.

Cephalic canal pores were counted in the manner described by Hubbs and Cannon (1935), transverse scale rows were counted according to the methods of Bailey (1959), and vertebral counts were made following the methods of Bailey and Gosline (1955).

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Figure 1. *Etheostoma boschungi*, new species. Paratype, UAIC 3973, adult male, 46.9 mm SL, from Copeland Branch, tributary to Briar Fork of Flint River, Madison Co., Alabama, 24 October 1970.

The methods of Hubbs and Lagler (1958) were employed in obtaining all other meristic and morphometric data.

We take pleasure in naming this new darter in honor of Herbert T. Boschung, Jr., Director of the Museum of Natural History, University of Alabama, in recognition of his contributions to ichthyology and his inspiration and devotion to his students.

Etheostoma (*Oligocephalus*) *boschungi*, sp. nov. Slackwater Darter

(Fig. 1)

Material.—The holotype, Tulane University, TU 79424, an adult male, 50.7 mm standard length, was collected from Lindsey Creek at the junction of Lauderdale County Roads 15 and 6, 0.8 mile north of Alabama Highway 20 at Central Heights, Lauderdale Co., Alabama (T1S; R12W; Sec. 3) on 22 November 1969 by Charles Gooch and James D. Williams. Of the 12 paratopotypes taken with the holotype, six specimens (32–55 mm SL) were deposited at the University of Alabama Ichthylogical Collection, UAIC 3774, and six specimens (43–50 mm SL) at Tulane University, TU 79425. Other paratopotypes were taken 22 December 1971 (TU 79427, 15:30–45); 29 November 1968 (UAIC 3210, 1:38); 7 December 1968 (UAIC 3204, 11:28–52); 25 January 1970 (UAIC 3961, 1:48); 22 March 1969 (United States National Museum, USNM 206421, 2:32–33); 19 July 1968 (USNM 206419, 1:46); 29 January 1969 (University of Michigan Museum of Zoology, UMMZ 197691, 3:29–34); and 19 April 1969 (University of Kansas, KU 14638, 8:30–36).

Paratypes include the following: Alabama—Lauderdale Co.: University of Florida, UF 18424 (1:40) Greenbriar Branch, trib. of Middle Cypress Cr. at Cloverdale (T1S; R12W; Sec. 26), 21 December 1968; UAIC 3206 (1:49) Lindsey Cr., 1.2 miles N of Ala. Hwy. 20 on Co. Rd. 5 (NE ¼, NE ¼, Sec. 30; T1S; R12W) 7 December 1968; UMMZ 197693 (2:42–46) Middle Cypress Cr. at Bethel Grove Church, just off Lauderdale Co. Rd. 11 (T1S; R11W; Sec. 5) 26 October 1969; UMMZ 197692 (2:47–51) Burcham Cr. on Natchez Trace Parkway (T1S; R12W; Sec. 31) 1 November 1969; USNM 206420 (6:28–33) Lindsey Cr. 0.6 mi N of Ala. Hwy. 20 on unnumbered dirt road (T1S; R13W; Sec. 24) 29 January 1969; University of Tulsa Museum, UTC 571 (2:31–37) Lindsey Cr. 0.6 mi N of Ala. Hwy. 20 on unnumbered dirt road (T1S; R13W; Sec. 24) 22 March 1969. Madison Co.: TU 79426 (6:36–46) Copeland Branch, trib. of Briar Fork of Flint R. on West Limestone Rd. (T1S; R1W; Sec. 26) 24 October 1970; UAIC 3973 (15:32–53) Copeland Br., trib. of Briar Fork of Flint R. on West Limestone Rd. (T1S; R1W; Sec. 26) 24 October 1970; UT 91.506 (4:28–34) West Fork of Flint R., Hazelgreen, 9 August 1969; UT 91.507 (1:20) Briar Fork of Flint R., 8 August 1969.

Tennessee—Lawrence Co.: Buffalo R., 9.9 mi N of Lawrenceburg on U.S. Hwy. 43. Florida State University, FSU 16408, 20 April 1969 (3:34–36); Mississippi State University, MSU 809, 11 March 1969 (1:34); UF 16537, 20 April 1969 (2:31–32); University of Tennessee, UT 91.101; 11 August 1967 (1:27); UT 91.331, 26 August 1969 (8:33–50).

The following material was used for comparison with *Etheostoma boschungi*.

Etheostoma cragini Gilbert. Kansas—Meade Co.: KU 3957 (19) Unnamed Cr. above Fish Hatchery, 14 June 1958; KU 8569 (57) Crooked Cr., 8 mi S and 2.5 mi W of Meade, 17 July 1964; UAIC 1810 (5) Crooked Cr., 8 mi S and 2.5 mi W of Meade, 17 July 1964; UMMZ 176858 (45) State Park, below dam, 26 June 1952; UMMZ 156694 (36) small stream, 1.5 mi N of Fowler, 1 January 1949. Sedgwick Co.: KU 12679 (10) Clear Cr. (T29S; R3W; Sec. 3) 13 July 1967. Stafford Co.: KU 12184 (14) Rattlesnake Cr. (T25S; R15W; Sec. 24–25) 1 April 1967. Missouri—Newton Co.: KU 7233 (2) trib. of Shoal Cr. at Neosho, 5 April 1961.

TABLE 1. Frequency distribution of lateral line scales, caudal peduncle scales, and transverse scales in *Etheostoma boschungi*, *E. pallididorsum*, and *E. cragini*.

Total Lateral Line Scales

	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	N	$\bar{x}$	SD
E. boschungi																				
Buffalo R.									4	2	2	2	1		2		1	14	52.57	2.93
Cypress Cr.			3	4	5	8	7	9	6	3	3	1		1				50	48.24	2.44
Flint R.		2	2	0	0	2	2	3	2	3	1	1	0	1				19	48.63	3.36
Total		2	5	4	5	10	9	12	12	8	6	4	1	2	2		1	83	49.06	3.11
E. pallididorsum			5	11	7	14	19	12	18	4	5							95	47.99	2.12
E. cragini	1	1	2	5	7	6	12	15	14	9	8	6	7		1	1		95	49.44	2.92

Pored Scales

	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	N	$\bar{x}$	SD
E. boschungi																		
Buffalo R.					1		3	4	1	2	1				1	13	37.70	2.46
Cypress Cr.		2	2	7	5	3	7	4	7	3	1	1	1			43	36.05	2.70
Flint R.	3	0	1	0	2	2	2	4	2	1	1	1				19	35.58	3.27
Total	3	2	3	7	8	5	12	12	10	6	3	2	1		1	75	36.05	2.87

	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	N	$\bar{x}$	SD
E. pallididorsum		1	5	10	15	18	15	12	8	8	5	1	2							100	12.86	2.39
E. cragini	2	3	2	3	4	6	8	8	8	7	13	11	9	6	2	2		1	1	96	15.37	3.77

Unpored Scales

	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	N	$\bar{x}$	SD
E. boschungi																		
Buffalo R.						1		1	5	1	2	1	1	1		13	15.00	2.16
Cypress Cr.	1		3	1	2	7	7	6	6	6	2	1	1			43	12.54	2.55
Flint R.				2	3	2	1	3	2	2	1	2	1			19	13.00	2.83
Total	1		3	3	5	10	8	10	13	9	5	4	3	1		75	13.08	2.69

	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	N	$\bar{x}$	SD
E. pallididorsum		1	2	1	2	6	9	9	14	8	8	8	10	7	5	5			95	35.17	3.29
E. cragini	1	3	3	3	7	7	9	12	13	10	10	3	3	2	3	2	3	1	95	33.86	3.70

TABLE 1. *Continued.*

	Caudal Peduncle Scales						N	$\bar{x}$	SD
	20	21	22	23	24	25			
E. boschungi									
Buffalo R.				4	6	1	11	23.72	0.82
Cypress Cr.		3	13	12	13	5	46	23.68	1.11
Flint R.			1	12	5	2	20	23.40	0.75
Total		3	14	28	24	8	77	23.40	1.03
E. pallididorsum	3	14	30	24	15	1	87	22.43	1.10
E. cragini	9	15	28	23	13	1	89	22.21	1.22

	Transverse Scales						N	$\bar{x}$	SD
	12	13	14	15	16	17			
E. boschungi									
Buffalo R.			3	11			14	14.79	0.43
Cypress Cr.	2	12	16	13	7		50	14.22	1.09
Flint R.			3	5	7	4	19	15.63	1.01
Total	2	12	22	29	14	4	83	14.64	1.14
E. pallididorsum	3	48	36	8			95	13.52	0.70
E. cragini	13	48	27	3			91	13.22	0.73

Oklahoma—Delaware Co.: KU 2416 (3) trib. of Elk R., 1 mi E of Turkey Ford, 22 June 1940. Mayes Co.: KU 6895 (14) Spring Cr., 1 mi S of Locust Grove, 27 June 1961; UAIC 1100 (10) brook trib. of Spavinaw Cr., 3.5 mi SE of Strange, 6 November 1950.

Etheostoma pallididorsum Distler and Metcalf. Arkansas—Montgomery Co.: KU 6158 (18 paratypes) small trib. of Caddo R., 1 mi W of Caddo Gap (T4S; R25W; Sec. 14), 6 April 1961; KU 6921 (32 paratypes) Caddo R., 8.5 mi W of Black Springs (T3S; R27W; Sec. 26), 28 June 1961; UAIC 1811 (3 paratypes) Caddo R., 1.2 mi W of Caddo Gap, 6 April 1961; UAIC 3516 (49 topotypes) Caddo R., 8.5 mi W of Black Springs on Ark. Hwy. 8 (T3S; R27W; Sec. 26), 17 April 1969; UAIC 3518 (16) trib. of Caddo R., 1 mi W of Caddo Gap (T4S; R25W; Sec. 14), 17 April 1969.

Diagnosis.—Distinguished from other members of the stippled darter (*Etheostoma punctulatum*) species group of the subgenus *Oligocephalus* by a combination of the following characters: bold, blue-black subocular bar; three prominent dorsal saddles, one on the posterior of the nape, one beneath the posterior of the first dorsal fin and one immediately posterior to the second dorsal fin. Vertebrae number 35 to 37, usually 36; pectoral rays number 12 to 14, usually 13; and pored lateral line scales number 30 to 44, usually 34 to 38.

Description.—Frequency distribution of scale, fin-ray, vertebrae, and cephalic pore counts for *E. boschungi* are given in Tables 1–4. Proportional measurements of the holotype and 11 paratypes are given in Table 5. The general body shape of *E. boschungi* is illustrated in Fig. 1.

The body is scaled except for the breast and prepectoral area. Nape squamation is generally characterized by small partially embedded scales which are usually more numerous on the posterior one-half to one-third of the nape. In a few specimens the nape is naked except for three to six embedded scales. The cheeks are naked. The opercles are naked except for one to six partially embedded scales along the posterior margin of the opercular flap immediately ventral to the opercular spine. These scales are absent in the Flint River population. The lateral line is incomplete with 30 to 44 pored scales. Unpored scales in the lateral series range from 6 to 19. Caudal peduncle scales range from 21 to 25, usually 23 or 24. Scales in transverse series range from 12 to 17, usually 14 or 15.

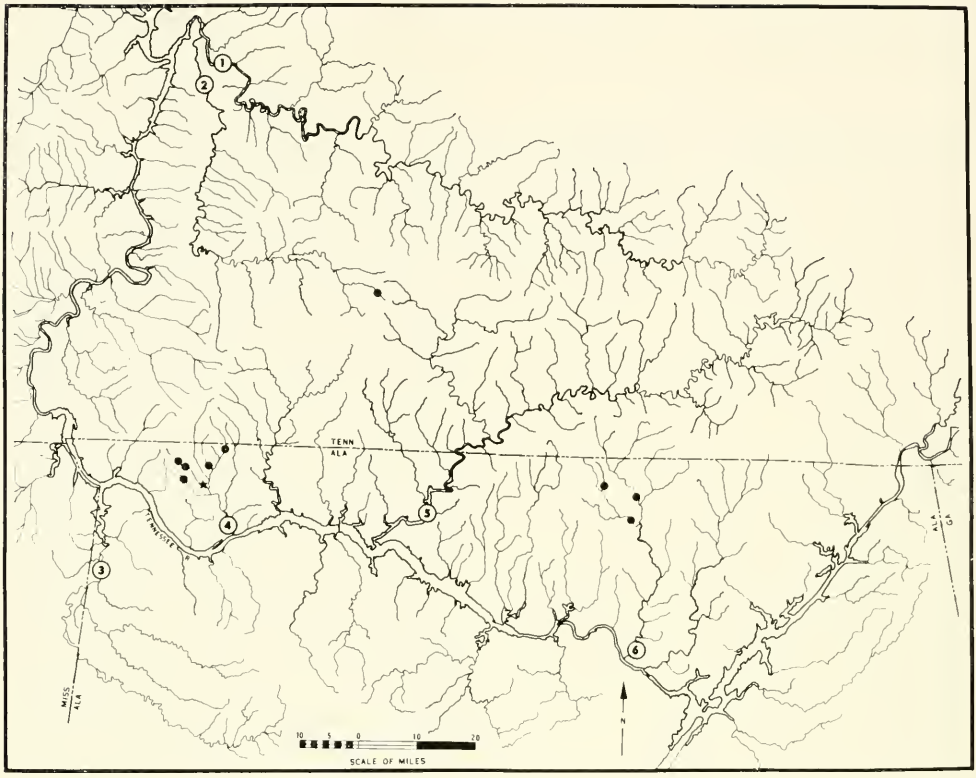

Figure 2. Distribution of *E. boschungi*. Star represents the type locality. Selected tributary systems of the Tennessee River are numbered: 1 Duck; 2 Buffalo; 3 Bear Creek; 4 Cypress Creek; 5 Elk River; 6 Flint River.

Dorsal spines range from 9 to 12 (usually 10 or 11); dorsal soft rays range from 10 to 13 (usually 11 or 12); left pectoral rays range from 12 to 14 (usually 13); and branched caudal rays range from 12 to 17 (usually 14 or 15). The anal fin typically has two spines and 6 to 10 soft rays (usually 8 or 9). Branchiostegal rays typically number six on each side. The branchiostegal membranes are narrowly joined to overlapping. The frenum is broad and well developed. Vertebrae in 28 specimens ranged from 35 to 37 (usually 36).

The infraorbital canal is complete and typically has seven pores. The preoperculomandibular canal is complete, usually with 10 pores. The supratemporal canal is widely interrupted, each branch usually having two pores. There is typically a single coronal pore.

Adult males with breeding tubercles have been taken in November, December, and January, but the tubercles do not appear to be fully developed. The maximum development observed thus far was on a male 43.5 mm SL taken at the type locality on 25 January 1970 (UAIC 3961). Tubercles are absent from the scales except for two to three scales around the anus which have a single small tubercle on each scale. Each of the anal spines and rays has a single row of tubercles which extends from near the base of the element almost to the tip. Tubercles on the anal spines are considerably smaller than those on the anal rays. The largest tubercles are present on the basal portion of the rays and these decrease in size toward the margin of the fin. Tubercles on the pelvic fin are present only on the basal two-thirds to three-fourths of the ventral surface of the outer two pelvic rays. All females examined lacked breeding tubercles.

Coloration of Males.—The following color description is based on specimens taken at

TABLE 2. Frequency distribution of fin rays in *Etheostoma boschungi*, *E. pallididorsum*, and *E. cragini*.

	Dorsal Spines									
	6	7	8	9	10	11	12	N	$\bar{x}$	SD
E. boschungi										
Buffalo R.				6	7	2		15	9.73	0.70
Cypress Cr.					18	34	1	53	10.68	0.51
Flint R.				5	13	3		21	9.90	0.62
Total				11	38	39	1	89	10.34	0.71
E. pallididorsum			7	59	33	2		101	9.30	0.62
E. cragini	1	2	16	52	24	1		96	9.03	0.80

	Dorsal Soft Rays						
	10	11	12	13	N	$\bar{x}$	SD
E. boschungi							
Buffalo R.		7	8		15	11.53	0.52
Cypress Cr.	1	25	23	4	53	11.40	0.68
Flint R.		2	16	3	21	12.05	0.50
Total	1	34	47	7	89	11.67	0.64
E. pallididorsum	2	39	43	17	101	11.74	0.76
E. cragini	10	51	34	1	96	11.27	0.66

	Pectoral Rays							
	9	10	11	12	13	14	N	$\bar{x}$	SD
E. boschungi									
Buffalo R.				4	8	3	15	12.93	0.73
Cypress Cr.				10	41	2	53	12.85	0.45
Flint R.				9	12		21	12.57	0.51
Total				23	61	5	89	12.80	0.53
E. pallididorsum		6	63	30	2		101	11.28	0.60
E. cragini	1	15	66	12	1		95	10.97	0.61

	Anal Rays							
	6	7	8	9	10	N	$\bar{x}$	SD
E. boschungi								
Buffalo R.		1	11	3		15	8.13	0.52
Cypress Cr.	1	8	30	14		53	8.08	0.70
Flint R.		2	8	10	1	21	8.48	0.75
Total	1	11	49	27	1	89	8.18	0.70
E. pallididorsum		38	56	7		101	7.69	0.60
E. cragini	22	68	6			96	6.83	0.52

	Caudal Rays									
	11	12	13	14	15	16	17	N	$\bar{x}$	SD
E. boschungi										
Buffalo R.				6	6			12	14.50	0.52
Cypress Cr.		1	3	38	5			47	14.00	0.51
Flint R.					17	3	1	21	15.24	0.54
Total		1	3	44	28	3	1	80	14.40	0.74
E. pallididorsum		2	20	51	20			93	13.96	0.72
E. cragini	3	18	40	22				83	12.98	0.80

the type locality on 22 November 1969, 7 December 1968, 22 December 1971, 25 January 1970 and from Copeland Branch (Flint River drainage) in Madison County, Alabama on 24 October 1970. Sexual dichromatism is pronounced in adults with the males being more brightly colored than the females. The most brightly colored male observed was collected 25 January 1970 at the type locality.

Table 3. Number of vertebrae in *Etheostoma boschungi, E. pallididorsum,* and *E. cragini.*

	33	34	35	36	37	N	$\bar{x}$	SD
E. boschungi			4	22	2	28	35.93	0.42
E. pallididorsum		1	24	6		31	35.16	0.45
E. cragini[1]	11	38	6	1		56	33.95	0.62

[1] Includes data from Bailey and Gosline (1955).

The olivaceous to brown dorsum is typically crossed by three dark brown saddles. The first saddle crosses the posterior part of the nape just anterior to the spinous dorsal origin. In some specimens the saddle extends ventrally to or just below the lateral line. The second saddle usually passes under the posterior-most spine of the first dorsal fin and touches the base of the first ray in the second dorsal fin. It extends ventrally to merge with the dark brown blotches along the lateral line. The third saddle is four to six scales wide and is situated immediately posterior to the second dorsal fin and extends ventrally to the lateral line. In some specimens there are one or two poorly defined saddles under the spinous and soft dorsal fins and one across the posterior portion of the caudal peduncle. These saddles are not as large or as intense as the three saddles previously described.

The dark brown to blue-black blotches along the lateral line are extremely variable in size and shape, but they are generally more prominent on the posterior one-half to two-thirds of the body. In some cases the blotches appear to be broken into several smaller blotches with light areas between them. In others, the larger blotches merge to form a very irregular band along the lateral line. There are usually a few scales with dark brown to black centers in the pale area above the lateral blotches. The pale dorsal and dorsolateral areas are suffused with light orange pigment which is usually more intense posteriorly.

Below the lateral blotches the ventrolateral and ventral surfaces of the body are suffused with orange pigment which obscures the underlying scattered melanophores. In the area where the ventrolateral orange pigment merges with the dark brown lateral blotches, the body is an iridescent greenish-yellow color. The orange color of the venter is more intense than that of the ventrolateral surfaces and is slightly more intense posteriorly. The anterior one-fourth to one-third of the venter has scattered melanophores which are more numerous and intense towards the base of the pelvic fins. At the posterior base of the pelvic fins the melanophores are concentrated into a narrow black band which extends dorsally along the posterior base of the pectoral fin, terminating just below the lateral line. The breast and isthmus are orange with scattered melanophores which are more concentrated on the posterior part of the breast, giving it a grayish-black appearance. The prepectoral area is light orange with scattered melanophores.

Table 4. Frequency distribution of cephalic canal pores in *Etheostoma boschungi, E. pallididorsum,* and *E. cragini.*

	Infraorbital Canal Pores						
	6	7	8	9	N	$\bar{x}$	SD
E. boschungi		56	2		58	7.03	0.18
E. pallididorsum		39	7		46	7.15	0.36
E. cragini	1	21	16	2	40	7.48	0.64

	Preoperculomandibular Canal Pores					
	9	10	11	N	$\bar{x}$	SD
E. boschungi	3	54	1	58	9.97	0.26
E. pallididorsum	9	36	1	46	9.83	0.44
E. cragini	2	33	5	40	10.08	0.42

Table 5. Proportional measurements of *Etheostoma boschungi*, expressed in thousandths of standard length.

	Holotype TU 79424	Paratypes ♂ TU 79425, UAIC 3961, UAIC 3774, UF 18424, UMMZ 197692 N = 6		Paratypes ♀ TU 79426, UAIC 3206, UAIC 3774, UMMZ 197692, UMMZ 197693 N = 6	
		Range	$\bar{x}$	Range	$\bar{x}$
Standard length (mm)	50.7	40.3–50.7	45.7	44.3–51.6	47.6
Body depth at dorsal origin	202	200–222	208	200–211	205
Distance from soft dorsal origin to anal origin	185	169–190	182	171–186	175
Caudal peduncle depth	114	101–114	109	107–112	109
Caudal peduncle length	231	222–236	229	233–249	240
Predorsal length	348	342–361	351	338–360	350
Spinous dorsal base	295	284–296	291	260–293	276
Soft dorsal base	184	151–184	172	151–177	166
Caudal fin length	220	197–225	211	207–217	212
Anal base	140	121–141	136	105–134	123
Longest dorsal spine	129	114–134	126	106–119	112
Longest dorsal soft ray	156	131–156	140	129–139	135
First anal spine	97	80–87	83	63–85	73
Longest anal soft ray	139	120–140	133	130–143	134
Longest pectoral ray	245	220–247	237	228–244	235
Pelvic fin length	219	200–219	211	186–214	204
Head length	321	305–324	317	303–318	311
Head depth at occiput	160	157–174	164	157–167	163
Tip of snout to junction of gill membrane	148	115–166	139	118–146	132
Junction of gill membrane to pelvic insertion	166	164–175	170	171–176	172
Upper jaw length	101	92–102	100	90–100	96
Snout length	79	67–82	76	71–79	76
Orbit length	75	74–82	76	71–82	76
Fleshy interorbital width	59	57–60	58	53–61	57
Snout tip to pelvic insertion	312	301–319	312	290–322	309

Dorsally the head is olivaceous to brown with some yellow-orange pigment present. The frenum and central portion of the upper lip are olivaceous. Laterally the upper lip is bright orange. The lower jaw is bright orange with scattered melanophores which are more numerous on the chin. The gular region, branchiostegal membranes, cheeks, and ventral part of the opercle are bright orange. Moderate to large melanophores are present on the cheeks and ventral surface of the opercle. Dorsally the opercle is olivaceous to brown and is suffused with orange pigment. A very bold blue-black subocular bar is present. The width of the bar is usually more than half the diameter of the orbit. A narrow dark brown to black postorbital bar is present just below the lateral canal.

The spinous dorsal fin has a blue-black marginal band which is very narrow on the anterior one-fourth to one-third of the fin, but gradually increases in width and intensity posteriorly. In some specimens the marginal band on the anterior portion of the fin is reduced to a small cluster of melanophores on the interradial membrane. Beneath the marginal band is a broad bright red-orange submarginal band. The band is approximately the same width throughout its length, but is slightly more intense posteriorly. The basal portion of the spinous dorsal fin below the submarginal red-orange band is bluish-gray to black. The soft dorsal fin has four or five longitudinal blue-black bars which are formed by concentrations of melanophores centered on the fin rays. The usual distributions of the bars are as follows: the first bar is marginal or submarginal; the second bar is just above the branching of the fin rays; the third is approximately midway between the second bar and the base of the fin; the fourth bar is at or just above

the base of the fin. The fifth bar, present in some specimens, is spaced between the second and third or third and fourth bar. The light area between the bars is suffused with a yellow-orange pigment which is most prominent on the anterior portion of the fin. In some specimens the first ray is light orange. The anal fin spines and interradial membrane are bright orange. Pigmentation of the anal fin is similar to that of the second dorsal fin except that the bars in the anal fin are more prominent. There are usually five or six dark bars on the caudal fin. The dark pigment of the bars is restricted to the fin rays. In some specimens the bars converge forming an irregular pattern. The pale area between the bars is suffused with yellow-orange which is slightly brighter than that of the second dorsal. The procurrent caudal rays are orange. On the pectoral fin, which is suffused with light yellow-orange pigment, there are usually six to eight dusky bars, poorly developed in some specimens. Usually, clustered melanophores form an oval blotch on the base of the pectoral fin. The pelvic fin has scattered melanophores on the rays and membranes which obscure the vague banded pattern when present. The melanophores are usually more numerous on the membrane towards the basal portion of the fin. Yellow-orange to orange pigment is most pronounced along the pelvic spine.

Coloration of Females.—In general, the pigmentation pattern of adult females is similar to that of males, but the intensity of the yellow and orange colors is greatly reduced. Melanophores along the ventrolateral and ventral surfaces of the body are larger and more numerous on females than on males. On the lower part of the cheek and opercle the melanophores tend to be grouped into small clusters forming a pattern of irregular blotches. In females, the blue-black suborbital bar is usually narrower and less pronounced than in males. The intense concentration of melanophores on the breast and the band of pigment that encircles the ventral half of the body behind the pectoral and pelvic fins of males is absent in females.

Habitat and Species Associates.—*E. boschungi* has been taken most frequently in clean, medium current, second and third order streams ranging in width from 10 feet to 20 feet, and ranging in depth from less than 6 inches to nearly 5 ft. With few exceptions, *E. boschungi* has been found to be associated with accumulations of leaves in areas of relatively low water velocity.

Of eleven specimens of *E. boschungi* taken from Lindsey Creek, 7 December 1968, seven were from loose accumulations of leaves, two were from a partially submerged tangle of roots, and one was from a marginal pool (8–10 in. deep) of still, clear water where the bottom consisted of angular chert rocks 1.5 to 2 inches thick. One specimen was removed from the stomach of a sunfish.

Three specimens were taken at the same locality on 29 January 1969, despite the fact that the water level was 10 to 12 inches higher than on 7 December and that many of the loose accumulations of leaves had either been washed downstream or had become more compact masses.

By 22 March 1969, most of the accumulations of leaves had been washed downstream. Two specimens of *E. boschungi* were taken in one of the few remaining masses of leaves.

There is a small spring (*ca.* 20 gpm) at the type locality whose waters flow a distance of approximately 60 feet before entering the creek. No specimens of *E. boschungi* were taken from the spring or the spring run by us or any other collectors. In view of the fact that *E. cragini* and *E. pallididorsum* typically inhabit springs and spring runs populated with herbaceous vegetation (Blair and Windle, 1961; Cross, 1967; Pfleiger, 1971), it is significant that *E. boschungi* was not found in the spring or spring run, nor was it found in any of the 67 springs of the southern bend of the Tennessee River system which were examined by Armstrong and Williams (1971).

A collection made in Lindsey Creek, upstream from the type locality on 7 December 1968 yielded a single specimen of *E. boschungi*. The bottom at this locality consisted of coarse sand overlain by large quantities of leaves.

Several collections were made at a point approximately 6 miles upstream from the type locality. Four of the six specimens taken from this locality on 29 January 1969 (USNM 206420) were taken from a pool which was *ca.* 25 feet wide and *ca.* 5 feet deep at its deepest point. These four specimens were taken from among leaves in the deepest portion of the pool. The other two

specimens collected on this occasion were taken downstream from the pool among leaves in water that was less than 2 feet deep. This locality was revisited on 22 March 1969, at which time we noted a reduction in the quantity of leaves on the bottom of the pool. A single specimen of *E. boschungi* was taken from the pool. A third visit to this locality on 4 October 1969, yielded no specimens of *E. boschungi*.

Although many of the 21 specimens of *E. boschungi* taken from Copeland Branch (Flint River drainage) on 24 October 1970, were taken from among leaves and from clumps of rooted plants, some specimens were taken from midstream areas where water flow was sufficient to prevent accumulation of leaves on the gravel bottom.

Known water temperatures during times of capture ranged from 7° C (22 December 1971) to 14° C (22 March 1969).

Specimens were taken on clear days (7 December 1968; 22 March 1969), a clear night (22 December 1971), and on days of rain (29 January 1969; 24 October 1970).

Species taken at the type locality in addition to *E. boschungi* include: *Lampetra aepyptra, Esox americanus, Hypentelium nigricans, Catostomus commersonii, Campostoma anomalum, Semotilus atromaculatus, Hemitremia flammea, Clinostomus funduloides, Notropis ardens, Notropis chrysocephalus, Fundulus catenatus, Fundulus olivaceous, Gambusia affinis, Etheostoma simoterum, Etheostoma duryi, Etheostoma squamiceps, Etheostoma flabellare, Etheostoma caeruleum, Lepomis cyanellus,* and *Cottus carolinae*.

Species taken at other localities in Lindsey Creek at which *E. boschungi* was taken include the species noted above as well as *Erimyzon oblongus, Chrosomus erythrogaster, Micropterus punctulatus, Lepomis megalotis,* and *Lepomis macrochirus*.

Species taken with *E. boschungi* in Copeland Branch include *Notropis chrysocephalus, Hemitremia flammea, Campostoma anomalum, Semotilus atromaculatus, Gambusia affinis, Lepomis cyanellus, Etheostoma squamiceps,* and *Etheostoma simoterum*.

Species taken with *E. boschungi* from the Buffalo River on 11 March 1969, include *Hypentelium nigricans, Campostoma anomalum, Clinostomus funduloides, Pimephales notatus, Etheostoma duryi, Etheostoma flabellare, Etheostoma squamiceps,* and *Cottus carolinae*.

Stomach contents of many centrachids were examined and one paratopotype (UAIC 3204) of *E. boschungi* (52 mm SL) was found to have been consumed by a *Lepomis cyanellus* (115 mm SL). Circumstances of capture and preservation were such that we are certain that the darter was not eaten by the sunfish in the seine or in the collecting jar.

Range.—Etheostoma boschungi is presently known from one locality in the headwaters of the Buffalo River in Lawrence County, Tennessee, six localities in the Cypress Creek drainage in Lauderdale County, Alabama and three localities in the Flint River drainage in Madison County, Alabama (Fig. 2). *Etheostoma boschungi* is the only species of the stippled darter (*E. punctulatum*) group known to occur in drainages east of the Mississippi River. Collecting efforts concentrated in the appropriate habitat in the Tennessee River drainage in north Alabama and west Tennessee may reveal the presence of additional populations. In recent years, however, intensive collecting in the Bear Creek system (Wall, 1968), Elk River system (Jandebeur, 1972), and 67 springs in the southern bend of the Tennessee River (Armstrong and Williams, 1971) yielded no specimens. These reports are based on a total of 300 collections.

Relationships.—Etheostoma boschungi appears to be most closely related to *Etheostoma cragini* Gilbert, 1885 and *Etheostoma pallididorsum* Distler and Metcalf, 1962. Blair (1964) suggested that the latter two species and *Etheostoma punctulatum* (Agassiz, 1854) comprise a natural species group. We agree and are of the opinion that *E. boschungi* is an eastern representative of this complex. The relationship of *E. boschungi* to *E. cragini* and *E. pallididorsum* is exhibited by similarities in the following characters: coloration of breeding males, distribution of breeding tubercles, certain fin ray, scale and cephalic canal pore counts, and general physiognomy.

The specific status of *E. pallididorsum* has been questioned by Ramsey and Suttkus (1965). We are of the opinion, however, that Blair's (1964) observations of behavioral and morphological differences in addition to data we have presented are sufficient to

support continued recognition of the specific status of *E. pallididorsum*. This problem will be explored more fully in a subsequent paper which deals with the distribution and relationship of all members of the stippled darter species group.

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